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HETEROSIS AND HOMEOSTASIS IN EVOLUTION AND IN APPLIED GENETICS

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The concept of crossing homozygous inbred strains anew each year to produce vigorous high-yielding combinations of hybrid corn was first proposed by George H. Shull in 1908. Theoretically it had many advantages over the older methods of seed selection. It made possible a much more complete control of the heredity in a naturally highly cross-fertilized plant. This finally resulted in the selection and use of superior germplasm. It also made possible the exploitation of the highest degree of hybrid vigor. This natural phenomenon was known to be important in many domesticated animals and cultivated plants, and particularly so in maize.

Notwithstanding these demonstrated advantages, the method as outlined by Shull and tested by numerous agronomists was not put into production due to very serious handicaps. Chief of these was the small size and variable shape of seeds produced on weak inbred plants. The cost of the seed was high and the performance was erratic, due to the handicap the plants had at the beginning of the growing season. Other factors also worked against the use of the uniform crosses of inbred strains as will be explained later.

E. M. East had started an inbreeding experiment with maize in Illinois in 1905, the same year that Shull began his experiments on Long Island. These experiments were continued when he transferred to the Connecticut Agricultural Experiment Station later the same year. Although no crosses had been grown between his two-generation self-fertilized lines, East immediately recognized the importance of the new method when Shull presented his results at a meeting of the American Breeders Association at Washington, D. C., in January, 1908.

At first both East and his student and successor, H. K. Hayes, made no headway with the commercial utilization of crosses of inbred strains and reverted to a method of crossing varieties originally advocated by W. J. Beal at the Michigan Experiment Station many years earlier. East had been employed as a chemist at the Illinois Station to make the analyses of the maize material being selected for chemical composition. In Connecticut he continued a similar selection program but in inbred lines of maize instead

of in naturally pollinated field plantings as in Illinois. Hayes developed this program further and added a number of new lines from the Illinois high and low protein selections of the Burr White variety and similar selections from locally adapted varieties of Leaming and Canada Yellow Flint. These experiments led directly to a method of maize breeding known as "Selection in Self-fertilized lines" described by the writer (Jones, 1920). This method, with various modifications by many corn breeders, produced the highly selected inbred strains now used for the commercial production of hybrid corn in all parts of the world.

The many inbred strains out of several distinct types of corn available at the Connecticut Station made possible a new method of combining self-fertilized lines. Tests had shown that crosses between varieties of corn of different type were usually more vigorous and productive than crosses made between varieties of the same type. This also proved to be true for the inbred strains derived from these varieties. Crosses of Leaming by Burr White inbreds or of inbreds out of High and Low protein selections of Burr White were usually noticeably more productive than crosses of inbreds within these varieties. Crosses of inbred flint or flour lines with each other or with dent inbreds were also sturdy in stalk growth and high yielding for grain. Fortunately crosses in all combinations of inbreds out of the available strains of Leaming and Burr White had been grown. From all of this evidence it seemed quite possible that a second crossing of a first generation hybrid of two Burr White inbreds by another first generation hybrid of two Leaming inbreds would be equally productive or even more so.

It was realized that this second crossing would be quite different from the first. All of the plants of the first cross are genetically alike where the inbred strains have been reduced to complete or nearly complete homozygosity. In the second cross all of the plants would be genetically unlike. Many of these individuals would be combinations of genes that had never been tested or even seen before. But if this second crossing would be approximately as productive, it might well be worth the extra effort since it would overcome most of the objections that had been found with the first cross. This second cross combining four inbreds, for convenience, was called a "Double Cross" to distinguish it from the first, or Single Cross, of two inbreds.

The first Double Crosses were produced in a small isolated field crossing plot grown at the Connecticut Agricultural Experiment Station farm at Mount Carmel in 1917. One of the best combinations of two Leaming inbreds was used as the pollen parent, being planted in every other row and in both outside rows. In the alternating rows were arranged 27 small plots. These seed parents, which were detasseled at the proper time, included various combinations of inbreds out of Burr White High and Low Protein selections and single crosses of other Leaming inbreds differing from the two inbreds used for the pollinator single cross. In addition, there were several F_1 crosses of dent × flour, dent × flint, flour × flint, flint × flint, and a few dent inbreds alone. The last items when crossed would give combinations

of three inbreds instead of four. Usually a hybrid of this kind, called a three-way cross, is made with the single cross as the seed parent to gain the advantage of high seed yields and large seed kernel. The object here was to compare multiple crosses of inbreds out of the same variety, some with a hybrid, others with an inbred seed parent.

All of these multiple hybrids were grown in a randomized yield test the following year. Most of them grew well and gave high yields. One of the combinations of two Burr White inbreds by two Leaming inbreds seemed to be most desirable on account of high grain yield, strong sturdy stalks and freedom from smut, aphis, and mold damage on the stalks and ears. This combination was called Double Crossed Burr Leaming. After testing for five years in Connecticut in comparison with all of the best adapted varieties commonly grown in the State and in many other places including Virginia, Ohio, Iowa, and Spain, it was put into commercial production by George S. Carter, at Carter Hill Farm, Clinton, Connecticut, beginning in 1921.

Later, another earlier maturing Double Cross called Canada Leaming was developed from inbred strains out of Canada Yellow Flint and the same Leaming pollinator. This with some modification was produced commercially by the Eastern States Farmers' Exchange beginning about 1930, and widely grown throughout New England and other northeastern states. In time both varieties were replaced by better double crosses as soon as these became available.

The greater genotypic variability of the double cross which, at first, was thought to be a serious objection, proved to be no handicap but, in fact, a further advantage. As measured by the coefficient of variation, the number of kernel rows on the ear and nodes per plant were somewhat more variable in the double cross than in the average of the two single-cross parents. Also, in weight of ear per plant the variability was slightly more but not significantly so. Height of plant and length of ear were less variable (Jones, 1922a). In every character measured, except rows of grain, the variability of the double cross was much less than the F_2 selfed generation of the parental single crosses.

In all details of plant structure the double cross was also much less variable than the original naturally pollinated varieties. All of the plants were uniformly productive (Jones, 1922b). The Burr Leaming hybrid showed no barren stalks and nearly all ears were about the same size and shape, and all of the plants were free from disease and insect infestation. All of the ears had a mixture of yellow and white kernels showing the genic segregation that was going on in these mixed populations.

Since all of the individuals in these double-crossed populations are uniformly vigorous and productive, all of the many diverse combinations of genes are heterotic. This is an important fact that I called attention to in the publication previously cited. This means that there are an enormous number of genes on all of the chromosomes involved in the heterosis shown by maize and other plants. If this were not the case the variability in

productiveness of the double cross would approach that of the F_2 self-fertilized generation from the same inbred parents.

Heterosis may be defined as the tendency for crossbred organisms to surpass both their inbred parents and their inbred offspring in some respect. The early hybridizers, Kölreuter, Gärtner, Focke, and many others, gave numerous examples of hybrid vigor in plants which is manifest in many different ways. They showed that the result of cross-fertilization may not always be beneficial to the organism. There is hybrid weakness as well as hybrid vigor. Within the species the result of crossing individuals that differ genically is usually an improvement in some respect. In general there are two different categories of effects. One that includes an increase in size or number of parts, and in rapidity of growth. This result is much the same as an improvement in environmental conditions such as better nourishment or better protection from unfavorable environmental factors. This effect has been called luxuriance. The second classification of effects includes all the factors that help an organism and its offspring to survive, for example, greater reproductive efficiency, disease and insect resistance, tolerance of unfavorable temperatures and other external influences of all kinds. This has been called true heterosis in contrast to mere growth luxuriance.

Naturally, applied geneticists have been more interested in the manifestations of heterosis that improve the organism itself, not only in its ability to grow and survive unfavorable environments but to take full advantage of all favorable environmental conditions that can be provided to both animals and plants so that their economic value can be enhanced. Students of evolution, understandably, are more concerned with the manifestations of heterozygosity and heterosis that enable organisms to compete and to survive under natural conditions. Many times these different results of crossing are antagonistic. Most cultivated plants are so highly selected for the production of food and other special purposes that they can seldom survive more than one or two generations in the wild. Domestic animals are also so highly specialized for meat, milk or egg production for food or for other purposes that they are severely handicapped in reproduction and survival even under carefully controlled conditions. Cross-fertilization among different types of these highly specialized domesticated forms usually results in a strong tendency to revert to a more nearly wild-type condition. They may produce offspring that are less productive but are usually better able to survive. This is particularly noticeable in crosses of the dairy breeds of cattle and of egg-laying strains of chickens. It was not until crosses were made of strains specially selected for productiveness in hybrid combination that the full advantage of heterosis was realized in both animals and plants.

The term heterosis was first used by Shull to designate the stimulus usually accompanying heterozygosity without any implications as to how this invigorating effect was brought about. There are two general interpretations of heterosis. One, the accumulation of dominant favorable genes at different loci. This accounts for much of the superior performance of hy-

brids. In addition to this there is also an interaction between different alleles at the same locus such that the final result is more favorable to the organism than the action of either allele in the homozygous condition. Direct evidence for intragenic heterosis is difficult to obtain. In view of the complexity of gene loci in bacteria and fungi, where it has been shown that there are numerous sites capable of cumulative action but cannot be recombined, it is difficult to distinguish between allelic and non-allelic interaction. For all practical purposes heterosis is an accumulation of favorable dominant effects. The position effect of cistrons is undoubtedly a factor in hybrid weakness but cistrons are relatively infrequent.

Heterozygosis is the usual result of amphimixis and may or may not be accompanied by heterosis. In most cross-breeding organisms the amount of heterosis remains at a fairly constant level and the organism is dependent upon it for survival. The genetic variability brought about by continued heterozygosity has long been recognized as one of the important factors in sexual reproduction. The ability of organisms to regulate and to utilize genic variability has been called genetic homeostasis by Lerner (1953). In 1944 I proposed the term genic equilibrium (Jones, 1944) to include somewhat the same idea. Darlington and Mather (1949) used the term genetic inertia. Whatever it is called, the concept of a regulatory mechanism that holds variability in bounds and enables an organism to survive is extremely useful and important. It is one of the most important factors in the success of hybrid corn and offers great promise for the further improvement of many naturally self-fertilized crop plants.

To illustrate the importance of homeostasis in hybrid corn let us compare a large number of single crosses made by crossing in all combinations a series of highly selected inbreds with a series of double crosses made from these single crosses. Such a comparison is available from field trials grown in various places in Iowa in 1951. These tests were carried out by G. F. Sprague, P. A. Miller, and L. H. Penny. The data are given in a mimeographed report entitled: "Iowa Experimental Corn Trials" and sent to the corn breeders in the various Corn Conferences in different parts of the country. The data in this report are particularly useful for this purpose as the tests were made in different parts of the State all in the same year. The fertility levels and weather conditions differed at the various locations but the yields obtained, ranging from 38 to 103 bushels per acre, indicate about average production for this most favorable part of the corn-growing region.

The inbreds used are the standard lines widely grown in the north central corn-growing area, selected from many thousands of inbred lines over many years of testing and observation under many different conditions. Along with these older lines are a number of new lines for comparison that were considered promising in preliminary trials. In other words, this series of inbreds is a very highly selected group and represents probably some of the most valuable maize germplasm that has been assembled to date.

From the performance of a series of inbreds crossed in all combinations it is possible to predict quite accurately the yield and other characters of

the many double crosses that can be made by crossing again these various single crosses. In the Iowa tests these predictions had been calculated and only a small proportion of the best of the many possible double crosses were actually made and grown. The comparison in yield of the two series of 317 single and 483 double crosses is shown in table 1.

In each group there is a high level of both heterozygosity and heterosis. In average yield the two groups do not differ significantly. The interesting difference is in the variability of yield. Both the two highest and the two lowest classes are in single crosses in which categories the double crosses are not represented at all. Not only is the range in yield wider in the single crosses but the frequency is distinctly bimodal. The double crosses form a more normal frequency distribution but with a decided skewness toward higher yields (figure 1).

TABLE 1

FREQUENCY DISTRIBUTIONS OF SINGLE- AND DOUBLE-CROSSED MAIZE HYBRIDS FOR YIELD IN BUSHELS PER ACRE

Class centers in bushels per acre	38	43	48	53	58	63	68	73	78	83	88	93	98	103	Total	Mean	S.D.
Single crosses	6	16	30	27	5	7	16	53	63	50	28	13	1	2	317	71.03	15.15
Double crosses			4	18	32	55	89	89	119	52	24	1			483	72.09	8.90

All corn breeders are familiar with the fact that the highest yields are usually obtained from single crosses when any large number are compared with multiple crosses. However, almost never is it the same single cross in any one year or in any one location that gives this high yield. The double crosses are more consistently high in yield and desirable in other respects as well, as compared to the single crosses which are more erratic in their performance. While genetically more variable in composition they are more stable and consistent in performance. That is why there are many double-crossed hybrids that are grown over very wide areas, some from Maine to Virginia and west to the Missouri River valley. There are varieties that grow well in the Southern states, in the San Joaquin Valley of California, in Spain, Italy, Israel and India.

The first double crosses were designed to overcome the handicaps that the single crosses had in seed production. It actually turned out that the genic equilibrium, genetic inertia, genetic homeostasis, or whatever it may be called, is by far the more important. It is the gyroscope that holds the ship steady in a surging sea.

Most of the genetic improvement that has been made with self-fertilized plants is based on the selection of pure lines as studied first by Hansen with yeast and Johannsen with beans. These genetically uniform pure line

varieties are very productive and highly desirable when environmental conditions are favorable and the varieties are well protected from pests of all kinds. When these external factors are not all favorable the result can be disastrous. Mixtures of pure lines have been proposed and tested by many agronomists (see review by Hayes, Immer and Smith, 1955). These mixtures usually do not give the highest yields at any time but may average higher

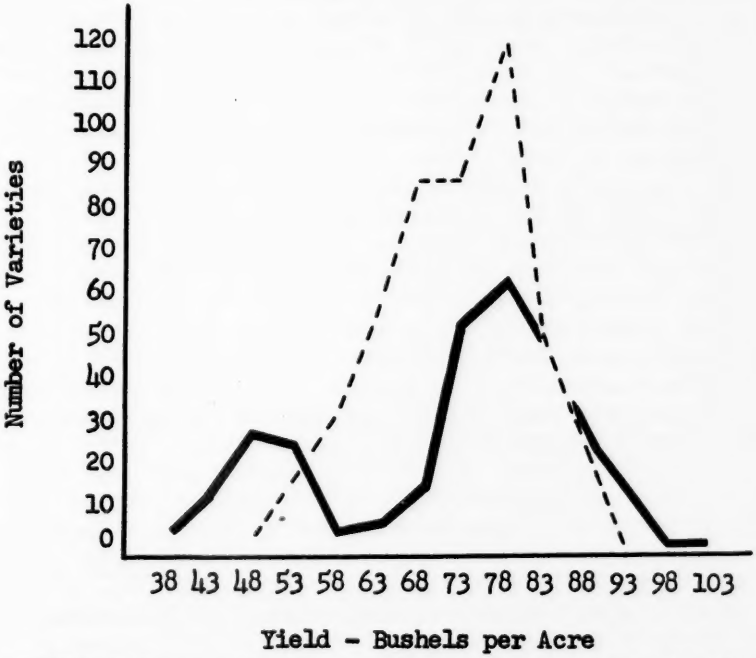

FIGURE 1. Frequency distribution of single- and double-crossed maize hybrids for yield. Solid line = single crosses, broken line = double crosses.

over a period of years. They are a form of insurance against very low yields or even complete loss due to some new virulent parasite. Silviculturists have found that mixed plantings of forest trees are usually safer than pure stands of one species.

Harlan, Martin and Stephens (1940), Sunneson and Stevens (1953), Sunneson (1956), and others have tested the crossing of pure lines of cereals and have found this to be advantageous. Starting with a small amount of intercrossed plants, the seed supply is built up rapidly in a few generations. This hybrid mixture has the advantage of both heterozygosity and heterosis, as well as a mixture of homozygous lines. Heterosis is lost rapidly in successive self-fertilized generations but enough of this invigorating effect remains after several generations to be worthwhile. The heterotic plants are more productive and tend to increase faster than the more homozygous indi-

viduals. Enforced heterozygosity tends to persist in all self-fertilized organisms whether naturally or artificially inbred.

Many ecological and genetic factors are involved in plant mixtures and agronomists have given considerable attention to this matter. Appreciable increases in yield can be obtained by hybrid mixtures, making the initial intercrossed seed each year and increasing this as fast as possible for field planting while considerable heterosis remains, using this seed for general field planting for only one generation. However, the mixture of genetically different types persists for many generations and can be used in several ways:

1. As a mixed population subject to natural selection in different locations, with the possibility of significant gains in yields from better adaptation over many generations.

2. As material for repeated hybrid recombination after periods of natural self-fertilization and consequent reduction in heterozygosity.

3. As a source of progeny selections. These new selections, after testing, may be used as pure line varieties or as material for a new mixed population with or without intercrossing.

Hybrid mixtures can do as much for naturally self-fertilized crops as crosses of inbred strains have done for cross-fertilized plants. There is every reason to believe that the importance of homeostasis will be recognized and utilized in applied genetics as well as it is recognized as a factor in evolution and survival under natural conditions.

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SELECTION, CONTROLLING FACTORS AND POLYMORPHISM

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The importance of ecology in evolution has been considered more in studying speciation than in other aspects. In general, it is thought that if two geographic races of a species have diverged and then meet they will probably compete; selection will then reduce the competition so that the two forms become ecologically independent and can live together in the same region. Now, I have argued (Williamson, 1957) that two species in competition share one or more controlling factors (population regulating factors). If this is correct, it follows that in speciation two forms change so that they no longer share controlling factors. This has many interesting consequences, but the point I want to raise here is that selection that relates to controlling factors will presumably vary in intensity with the size of the population, but none of the mathematical theories of natural selection consider this. In this paper I will discuss some of the possible interactions between selection and population size in relation to polymorphism and the consequences of these on the use of polymorphism in detecting competition. Sheppard (1956) has discussed other important aspects of this subject. There are, however, two topics that must first be mentioned. These are the cases in which selection has been thought to change with population size and the meaning of the word interaction when applied to selection and controlling factors.

Changes in selection with population density have been shown experimentally by Birch (1955), who suggested that he had found an explanation of the seasonal changes in the frequencies of chromosome inversions in some Drosophila. Several reputed cases of such selection changes in wild populations have been reported. The animals involved are the earwig *Forficula auricularia*, the moth *Panaxia dominula*, the butterfly *Melitaea aurinia*, the fox *Vulpes fulva*, the hamster *Cricetus cricetus* and the dove *Columba livia*. Four of these can be quickly dismissed. Huxley (1955, 1956) has claimed that both sex-ratio and the proportion of long forceps change with population density in the earwig. The only evidence on sex-ratios in comparable populations (Fox-Wilson, 1940) does not support him; the dimorphism in forceps may well change with density as it seems, as Huxley himself showed (1927), to depend on growth rate and not on genetic segregation. For the fox, Butler (1945, 1947, 1951) has argued that all changes associated with cycles can be explained by migration. Until this has been disproved these changes cannot be ascribed to changes in selection pressure. Ford (1945) suggested that there might be a relation between selection and population in Panaxia but later work by himself and Sheppard (Sheppard, 1956) showed that a constant selective value since 1939 gives a satisfac-

tory fit to most of their figures and that selection is not a function of population size. In the Faroes, the Rock Dove has a polymorphism which is unusual in that the recessive allele, which gives a dark bird when homozygous, is rarer than the dominant. Petersen and Williamson (1949) thought that dark birds were commoner at high populations, but this conclusion is based on two years' figures so that a causal connection between numbers and gene frequency would not be proved even if there had been a significant change in the proportion of darks. If the change had been from 7 dark and 93 normal to 20 dark and 120 normal, the probability that there had been no change in the population is over 0.9; on the other hand a change from 6 : 114 to 34 : 204 has a probability of less than 0.02 of occurring by chance. Both sets of figures are possible from the data given, so it is not even certain that there was a real increase in the proportion of darks in 1936–37.

The remaining two cases are more satisfactory. Gershenson (1945) showed that there was a correlation between numbers and the proportion of melanics in hamsters, and that the partial correlation eliminating predators was also significant. It is a pity that he did not calculate all the possible partial correlations or give the figures so that this could be done; without these statistics the importance of predators in determining either population size or melanic frequency is uncertain. Ford and Ford (1930) showed that variation was greatest when the population of the Marsh Fritillary was increasing fastest. There is an unexplained observation that in the first year of increase all were "extremely dark" and "more or less deformed." A simple relaxation of selection should merely increase the variation around the mode; the sharp change of mode must have been due to some other cause, such as an important change in the habitat or hybridization between two colonies. It is also uncertain how much of the variation they observed was genetic.

The evidence that selection changes with population size is, then, very slender. Even so it is necessary to be quite clear how the two might interact, and on this there is the possibility that some statements by Haldane (1953, 1956) and Sheppard (1956), though perfectly correct, may be misunderstood. Haldane in his first paper says "The survival of the fittest will only cause the number of animals in an area to increase if the fitness concerns a negative density-dependent factor." (Haldane uses 'negative density-dependent factor' for what I am calling 'controlling factor.') The misunderstanding would arise in the interpretation of 'concerns.' Consider a population living in a constant uniform environment and with all individuals alike, a population like that discussed in Williamson (1957). The size of the population is determined by the balance of births and deaths. Suppose that the birth rate is constant and death comes from one controlling factor and another factor which acts at a constant rate. Then the system is

$$\mathrm{d} \ln n/\mathrm{d}t = b - \mathrm{f}(n) - d$$

where n is the population size, t time, b and d are constants to represent births and non-controlling deaths and $\mathrm{f}(n)$ is a monotonic increasing func-

tion of n and represents the controlling factor. At equilibrium $f(n) = b - d$, so that any change in d will change the equilibrium density. However, as deaths from d and from the controlling factor are taking place at the same time they may be said to 'concern' or 'interact with' each other. Consider next a more complicated case of an insect with larval and adult stages and with a controlling factor acting only on the larva. Then non-controlling deaths of the larvae can cause either an increase or a decrease in the population depending on how they interact with the controlling factor. Variation in the adult death rate will always affect directly the numbers of adults in such a system, but even considering only the numbers of larvae, deaths of adults would have no effect on the numbers only if the controlling factor was of the overflow type, always bringing the population back to one fixed density in the same way that an overflow on a tank brings the water level to one constant height. Other sorts of controlling factors would be affected by changes in larval number caused by changes in the adult death rate. It is perfectly reasonable to say that in the overflow factor case adult deaths do not concern or interact with the control, and that in other cases they do, but evidently considerable care must be taken in discussing these interactions.

It is now possible to discuss the effects of variations in selection on polymorphism. There seems to be no complete list of the known mechanisms for maintaining polymorphism; and as many of these mechanisms involve variable selection coefficients such a list may serve to emphasize the considerable possibilities resulting from variable selection. Polymorphisms with constant selective values have sometimes been described as involving a balance of selective forces. This is misleading as can be seen by distributing the selective values over the genotypes in other ways. For instance, in the case of a polymorphism maintained by heterozygote advantage, the stability comes from the fact that the selection coefficient of the heterozygote is greater than that of either homozygote. If these three coefficients are allotted to the three genotypes so that one of the homozygotes has the largest, then no polymorphism results. The balance is in fact often between the selective forces and the genetic system. It is true that in these systems there is a tendency for a gene to increase if it is below the equilibrium frequency and decrease if above; this is not a cause but an effect. There is no need to discuss most of the types of polymorphism here, further information can be got from the references. These references are added to indicate precisely what system is meant; they are not meant to be exhaustive or to assign priorities. I have not included the self-sterility allele system, as none of the genotypes can be recognized by inspection. However, such alleles could presumably be involved in a polymorphism of type A. 3. b. below.

A. Constant selective values.
  1. Depending on simple segregation.
    a. Heterozygote advantage.

b. Systems of multiple alleles. Owen (1953), Kimura (1956a).
c. Interactions between loci. Kimura (1956a).

2. Depending on abnormal segregation. e.g. sex ratio in Drosophila (see White, 1954) or *t* locus in mice. Bruck (1957).
3. Reacting with other polymorphic systems.
   a. with sex dimorphism. Owen (1952).
   b. linked to a polymorphic locus. Kimura (1956b).
   c. with sex linkage. Haldane (1954), Sprott (1957).

B. Variable selective values.

1. Selective values vary in space or time.
   a. Clines.
   b. Cyclical seasonal changes.
   c. Levene's system. Levene (1953).
2. Selection depends on the frequency of other individuals of the same species.
   a. Sex.
   b. Other outbreeding systems. Finney (1952), Lewis and Crowe (1956).
   c. Mating preferences. Sheppard (1952), Tebb and Thoday (1956).
   d. Compensation, as may occur in Rhesus blood groups. Lewontin (1953).
3. Values depend on biotic variables which may or may not be part of the polymorphic species.
   a. Commoner form at a disadvantage. Wright and Dobzhansky (1946), Lewontin (1955).
   b. Selection for diversity, as has been suggested for mimetic polymorphisms. This system has not been analyzed mathematically.
   c. Labile pathogens. Haldane (1954, case 7).
   d. Cases analogous to balanced competition. Williamson (1957).

Of all these only the last case, B. 3. d., involves selection varying with population size, but the commonness of a type is in no way indicated by the number of other possible types, and furthermore a polymorphism may involve more than one mechanism.

The last topic to consider is the possibility of using polymorphism as an aid in detecting interspecific competition. In Williamson (1959) I have pointed out that competition might be detected by the existence of a significantly negative partial correlation between two species, using a suitable measure to eliminate the effects of habitat differences. The question is whether polymorphism can be such a measure.

If two species are in competition, that is if they share a controlling factor, and one or both of them is polymorphic, the frequencies of the morphs will be affected by the competition only if it is of type B. 3. d. In simple cases the converse will be true; that is, the competition will not be affected by the polymorphism except when the same controlling factors affect both. For practical purposes this will hold in some more complicated cases, such

as when polymorphism changes the birth rate of a species in different habitats in a way not to be expected in a monomorphic species. In an analysis of the type suggested in Williamson (1959) this will merely make the habitat appear to vary in a peculiar way. However Sheppard (1956) has pointed out that there are other cases in which polymorphisms not of type B. 3. d. will affect the outcome of competition. Even without these complications, polymorphism must be used quite differently in detecting competition depending on whether or not it involves controlling factors. If the polymorphism is independent of population density, the phenotype frequencies in different places can be used as a measure of the habitat for calculating partial correlations between two possible competitors eliminating the habitat. The theory of this is explained in Williamson (1959). Polymorphism is no more and no less likely to be useful in this way than any other measure, though it will usually be more easily recorded.

The detection of competition when polymorphism interacts with the population controls is never likely to be easy. Consider a situation in which a polymorphism is maintained in a species by a balance between two controlling factors, and that one of these factors also controls another, monomorphic, species. The species are thus in competition with respect to the second control. The frequency of the forms in the first species will depend on the density of the second. Consequently the partial correlation between species numbers eliminating the polymorphic ratios will be nil, and in that sense the polymorphism hinders the detection of competition. However, the other two partial correlations, between the numbers of each species and the ratio of the forms, will also be nil, and this will at least indicate the possibility that all three variables must be considered together.

The study of the variations in polymorphism in one species will be of more direct use in studying ecological processes when more is known about the way in which particular polymorphisms are maintained. Population dynamics, which is a term much abused by geneticists and by which I mean the study of the size and changes of populations, may, conversely, be of importance in work on polymorphism. At any rate, as polymorphism offers one of the easiest ways of studying selection, and as population dynamics has been almost entirely neglected in theories of evolution, combinations of the two are likely to be of great interest and importance.

SUMMARY

Speciation requires a change in the controlling factors of one or both of the species concerned, and so involves selective forces which vary with population density. The only good field evidence for such selection is Gershenson's on the hamster. The results of the interaction of selection and controlling factors vary with different systems of control.

The mechanisms known to be able to maintain a polymorphism are listed. Many of them involve variable selective coefficients, but only one needs selection varying with population density. The use of polymorphism in detecting competition depends on the way the polymorphism is maintained.

When the genetic system is independent of population density the usage is straightforward; when it is not, the results of the correlation analysis may only demonstrate the dependence.

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THE BIOLOGICAL ADAPTATION OF MAN TO HOT DESERTS

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CLIMATIC ADAPTATION

Modern man lives in almost all parts of the terrestrial globe. We attribute this wide distribution to his culture and believe that biological man is a semi-tropical animal who, without culture, could operate only in a very narrow temperature range. Technology has, undoubtedly, widened the temperature range within which man can live. Yet, with a very simple technology, man lived in such widely divergent climates as the Sahara desert and the wet-cold of Tierra del Fuego. While these groups had tools to help them in quest of food, their cultures provided very little protection from the climate. Even modern man should not be visualized as free of his climatological environment; rather, modern culture might be thought of as an insulation against the environment, mitigating but not destroying the climatological forces that act on human biology. This is particularly true of the desert where clothing does not greatly alter the effect of the climate on man.

In the desert, man may wear boots to protect his feet from the hot ground and clothing to reduce the radiation received on the body, but he remains basically dependent on his inherent heat dissipation mechanisms for survival. These mechanisms vary widely between men so that no two men are exactly alike in their ability to perform work in the heat. The obvious extremes are individuals born without sweat glands and those who can perform hard work when the desert temperature is even as high as 110°F. Those men without sweat glands never survive in hot environments, but what of the so-called "normal" man? In many cases within a group of healthy and apparently "normal" men working in the desert one will suddenly collapse and die of heat stroke (Schickele, 1947), even though he was apparently performing the same work under the same external heat load as his fellow men who suffered no ill effects. Under standardized work conditions in the desert, individuals vary by as much as 100 per cent in their sweat loss, two degrees in rectal temperature, and 50 pulse beats per minute (Adolph, 1947). These ranges often signify the difference between continued work and collapse. The large between-individual variation in response is not strongly affected by recent nutritional, work, or disease histories. Instead, the response is reproducible, that is, it can be measured in successive trials at approximately similar magnitudes even when several weeks' time have passed. Thus, it appears that the major amount of individual variation in resistance to heat is a product of inheritance plus life-long environmental adaptation. These factors cannot be modified in most cases, but by dis-

covering them, it should be possible to classify a man's ability to withstand desert heat stress before he is actually placed in the stressful condition.

It appears that the final tolerance of men exposed to desert heat stress depends on biological tolerance. Psychological and cultural factors have a large influence on man's ability to prevent exposure to severe heat, but if exposure is inescapable for a group, man's biology limits his tolerance. For this reason a search for adaptation to heat must logically rest on a biological, not cultural, criterion. In actuality, no biological characteristic is free from cultural influences, and the physiological reactions of the man who finds himself in severe heat are modified by both his individual and cultural background. However, the use of biological measurements such as body temperatures are, without doubt, much more indicative of physical condition than the subjective judgments of either the subject or an observer.

In the present study rectal temperatures, pulse rates, and sweat losses, as well as heat stroke, have been used as indices of heat tolerance. Most of these variables are at best only indirect measurements of heat tolerance. With so many limitations already imposed on the criteria, it would be desirable to compare directly populations under desert heat stress conditions. As this is virtually impossible, this study attempts to construct a partial biological model for desert heat resistance. In this study the word model is used to connote ideal. That is, on the basis of the adaptive mechanisms utilized by the human body, what kind of man would be the most perfectly adapted to hot desert thermal conditions? Using the concept of a biological model, the major problem of how man adapts to a hot desert climate may be subdivided into three phases:

1. Are there human morphological and racial variables which increase or decrease desert heat stress tolerance?
2. If these variables exist, what are the respective influences of the genetic and environmental forces on the adult phenotypic manifestation?
3. How does the theoretical biological model compare with the actual world distribution of morphological and racial characteristics?

THE NATURE OF HEAT STRESS

The responses of the human organism to hot desert stress may be divided into two major categories: (a) *Responses referable to man's thermoregulatory mechanisms*; these may be termed systemic in that they affect the total body, and should be considered primary because the regulatory mechanisms must be adequate for the stress level or a serious performance decrement: sometimes death will result. (b) *Responses of a non-thermoregulatory nature*; beside the primary strain of temperature regulation, the desert produces several secondary forms of strain in the sense that they affect only limited portions of the body and are not directly lethal, for example, eye strain, sunburn and extremity swelling.

In this study these many secondary strains have not been considered and attention was focussed on the primary problems of temperature regulation.

The ability of a group of men to survive in the desert also depends on their being able to withstand secondary stress. However, for survival, adjustment to the severe systemic heat stress is of primary importance and is less subject to mitigation by technological aids.

The effects of desert heat on man are qualitatively as well as quantitatively different from the effects of hot wet climates. The external heat load on the individual in the desert is several times greater than it is in a hot jungle. In the jungle, dry bulb temperatures rarely exceed inner body temperature, while on the hot desert the reported temperature frequently is 10° to 20°F. higher than the body temperature. Even this comparison does not present the full difference between jungle and desert dry bulb temperatures. Conventional temperature readings are taken at four to five feet above the ground. In the wet tropics the ground temperature equals or is below the reading taken at four feet. In the desert, ground temperatures are much higher than four-foot temperatures. At Yuma, Arizona ground temperatures were found to run as high as 150°F. (Yuma Handbook, 1954). At one foot and two feet above ground level dry bulb temperatures were still found to be two to three degrees higher than at the 48 inch level. These statistics indicated that in terms of man's micro-climate, the temperature contrast between the jungle and desert is even greater than is apparent from official temperature records.

There is, then, a decided quantitative difference between the heat loads of the tropics and the hot deserts. Yet the body heat storage and psychomotor performance are not substantially different between these climates. Man's ability to function as well in the hot desert as in the tropics is related to the nature of his cooling mechanisms. As long as the ambient dry bulb temperature is lower than man's core temperature, some of the heat of metabolism is lost by radiation, convection, and conduction. The quantity of heat loss by these mechanisms depends primarily on the area of temperature contrast. Thus, if the skin temperature is 96°F. in a 90° environment, the heat loss from the body is greater than if skin temperature is 94°. In the heat it is, therefore, advantageous for man to have a high skin temperature and maintain a maximum rate of heat exchange between the deep body and the subcutaneous area. Several body mechanisms speed up this heat exchange when the individual is subject to heat stress. There is a general peripheral vasodilation allowing maximum surface blood flow, which brings the deep metabolically produced heat to the surface and carries back the cooled blood (Bass et al., 1955). However, the heat production of the body even under basal metabolic conditions exceeds the heat loss by radiation, conduction, and convection when the ambient temperature reaches about 85°F. A working man exceeds this potential at a much lower ambient temperature. When the body heat production exceeds loss through these mechanisms, then new avenues of loss must be utilized or the organisms will start to accumulate heat. A small heat accumulation can be tolerated by the body, but for the rare individual born without sweat glands adaptation

ends here. Without the sweating mechanism man could not survive for long in environments over 85°F.

Although the ambient temperature reaches 120°F. in the desert, the dry bulb temperature just above the surface of a man's skin is below subcutaneous temperature due to sweat evaporation. Each gram of water absorbs 0.578 calories of heat when it evaporates on the skin. The total heat loss by sweating is thus determined by the amount of sweat produced and the ability of the environment to evaporate the sweat. While the sweat production of the body keeps close to cooling needs, the ability of the environment to vaporize water is dependent primarily on the wet bulb temperature and the size of the skin area over which the water is distributed. It is in the wet bulb temperatures or absolute humidity that we find another large difference between the tropical and the hot desert climate. While the dry bulb temperature of the desert is much higher than a tropical area, the wet bulb temperature is similar or even lower and thus in desert climates sweat evaporation is complete, while incomplete in tropical areas.

An analysis of the stress imposed on man by heat has indicated the necessity for distinguishing between the heat stress of the desert and the tropics. To summarize these differences we may say that the hot desert imposes a quantitatively greater heat load on man but because all sweat is evaporated in the desert, the body heat loss is limited only by the body's ability to produce sweat. In the tropics, however, where only limited quantities of sweat can be evaporated, heat loss is governed by the surface area of the individual. These statements are, of course, an oversimplification but do indicate some of the differences between the impingement of tropical and desert heat stress on human thermal regulation.

THE HUMAN BIOLOGICAL MODEL FOR HOT DESERT TOLERANCE

There is considerable variation in human desert heat tolerance which occurs in healthy individuals and is probably species wide. How important this variation is for the survival of an individual or group is quite obviously a function of the culture. In present American society a man can survive and propogate in the hottest desert area even if he has a very low tolerance of heat. However, in an agricultural or hunting culture heat tolerance becomes more critical. Even within certain segments of our own society, such as the military, desert heat tolerance may be very important for individual survival.

The most definitive criteria of desert heat tolerance is death, or no death, from exposure to high heat stress. The only available published material of this nature was reported by Schickele (1947). She reported on 147 deaths from heat prostration. These deaths occurred during the training and maneuvering of soldiers in desert areas. From the medical records of these men she obtained height and weight data and compared these data to that found for 100,000 randomly selected soldiers. Her results indicated that the higher a man's relative body weight, the greater his susceptibility to fatal

heat stroke. The maximum probability of fatal heat stroke was among men 55 or more pounds overweight. This was a trend over the whole scale of relative weight so that men 5 to 14 pounds above normal were four times more susceptible to fatal heat stroke than men of average weight. Even the men with an average relative weight were four times more susceptible than men 16 or more pounds under the average for their age and stature.

Weight deviations from a standard reflect both fat and muscle variation, but for individuals of the same racial and cultural background these deviations primarily reflect variation in adiposity. Thus Schickele's data indicates that the greater a man's adiposity, the lower his heat tolerance. It also suggests that a large muscle mass for a given stature reduces a man's desert heat tolerance.

Lacking survival data on which to base an adequate model, physiological data offer the next best criteria. Information on body temperature, sweat loss, and pulse rates indicate the level of strain which a man is experiencing. Presumably the strain level has a relationship to how closely a man is approaching collapse. It probably also has some significance on the man's performance potential. Studies using physiological criteria showed the same results as Schickele's data (Baker, 1955). Using a direct measurement of fat, it was found that fatter men had higher strain levels. It was also found that men with compact bodies (low stature per unit weight) had lower tolerance of heat. Physiological data also indicate a skin color factor in heat tolerance. The dark skin when exposed to solar radiation, absorbs more energy and thereby raises the strain level (Baker, in press). On the other hand, a very light skin does not tan and therefore, leads to a much greater strain on the man when exposed to the sun for any extended time span. Thus, brunette skin which is capable of tanning, but has a minimum absorption of solar energy is the most adaptive skin color. In addition to skin color, there appear to be other racial factors involved in heat tolerance. These factors have not been isolated so that present evidence only indicates that Negroes have a greater physiological tolerance of hot wet conditions, but because of dark skin color do not have as great a tolerance of hot desert conditions (Baker, in press).

In addition to these morphological and racial criteria of heat tolerance, the physiological mechanism termed acclimatization must be included in a model. Bass et al., (1955), have demonstrated that men drastically improved their ability to perform work in the heat after working for two weeks under hot conditions. Acclimatization is presumably a universal phenomena in man and, if so, it would appear to be a genetically inherited mechanism mediated by heat strain. However, to date, work on this mechanism has not indicated how much variation may exist between individuals and groups in their ability to acclimatize.

From the above characteristics a partial model may be constructed for desert heat tolerance. The application of this model does not predict all of the between-individual variation in heat resistance, but does indicate some of the important morphological and physiological features which charac-

terize a man with high desert heat tolerance. The man should have low subcutaneous fat, large surface area per unit weight, brunette skin color, and be acclimatized to a high level.

THE GENETIC AND ENVIRONMENTAL BASIS OF THE BODY CHARACTERISTICS INVOLVED IN HEAT TOLERANCE

The basic characteristics by which man adapts to heat are genetically determined. The human infant shows most of these physiologic mechanisms at a very early age. He vasodilates and constricts, sweats, and increases blood flow with heat stress. In the very first days after birth these mechanisms are weak and sometimes completely fail. This may be a very important consideration for population size in the desert. Also, it seems quite probable that if adequate demographic data were available on hot desert populations, the per cent of the population born in the hot season and surviving to one year would prove to be much lower than comparable statistics for those born during the cool season. Despite the inadequacy of the newborn's temperature regulatory mechanisms, we have no evidence to suggest that prenatal environment has played an important role in modifying these mechanisms. Post-natal environmental effects on temperature regulatory mechanisms are equally unexplored. Therefore, investigation of the genetic and environmental influences on heat stress resistance is limited to an exploration of the characteristics which have been found related to the heat tolerance.

Skin Color

Skin color is primarily an inherited characteristic with a secondary environmental effect depending on ability to tan. It has been shown that variation in dermal melanin is the primary variable in solar energy absorption and also represents most of the racial variation which is observed in skin color (Edwards and Duntley, 1939). Tanning is a secondary increase in dermal melanin in response to certain wave lengths of radiation and is found in people who are in the mid-range of skin colors. Individuals with very high skin melanin content do not increase their melanin enough to produce a significant change in solar radiation absorption, while individuals with very pale skin appear incapable of tanning, thereby rendering them incapable of prolonged exposure to the sun.

Tanning data collected at Yuma, Arizona, on soldiers (unpublished data) indicated that the average White, when tanned, absorbed 13 per cent more solar radiation than when untanned, while the American Negro skin only changed by 6 per cent. This suggests that within certain limits the higher the amount of inherited skin melanin, the less the solar radiation absorption will be affected by tanning.

Body fat

The fatness of men is one of the characteristics which shows the greatest susceptibility to environment. However, there appears to be a genetic in-

fluence on the distribution of body fat even if the quantity is environmentally controlled. The most obvious evidence of inherited fat patterning is the Bushmen. The steatopygic pattern of fat deposition may be an adaptive feature in that stored energy in the form of fat is available, yet the fat is not deposited equally over the body in such a way that it would act as insulation. In recent family studies on White Americans, Garn (1955) found evidence for familial patterning of fat deposition. While no evidence can be cited, it is quite possible that the location of fat deposits even in non-steatopygic populations may be important in heat tolerance.

Stature

Inheritance is undoubtedly important in stature determination but environment can grossly modify the phenotypic development. It is usually accepted that genetic constitution sets a limit for the adult height of a specific individual while environment only controls how near one attains the genetic maximum. The recent generation increase in the stature of Europeans and Americans makes this concept tenuous because we would now have to assume that very few of us are attaining our true genetic potential (Trotter and Gleser, 1951). A more complex genetic inheritance of stature should be proposed; a more realistic view might be that stature attainment is not directly inherited, but is a secondary attribute resulting from the patterning of inherited endocrine function. Within such a system environmental forces could easily act to decrease, increase, or even stop the inherited directed growth. The most obvious example of environmental effects is the anomalous growth that frequently results from damage to the pituitary gland.

Fat-free weight

The adult fat-free weight as well as the stature of a man appears to be an indirectly inherited characteristic, that is, one determined by genetically directed growth potentials which act through the environment of the organism. However, fat-free weight is more subject to environmental modification probably because of the involvement of more genes, and more opportunity for environmental infringements. Climatic factors alone seem capable of exerting a strong influence on body weights even within racial groups. Newman and Munro (1955) found that, comparing the genetically similar State populations within the United States, there was almost a twenty-pound weight difference between the coldest and hottest States. Roberts (1953) similarly found á weight to climate relationship within the British Isles. In both cases the genetic compositions and cultural factors may vary somewhat with climate but the size of the weight difference suggests a rather direct biological influence of climate on weight.

From studies on men moving into hot areas for short periods, it appears that the effect of climate on the weight of a group is not a rapid short-term process (Baker, 1955). Instead, the fact that the subjects studied by Newman and Munro (1955) were in their early twenties suggests that the climatic influences manifest themselves during growth. The studies of Mills

(1942) on the growth of American children in Panama support this hypothesis. It is unfortunate that so little information on this subject can be drawn from the numerous growth studies in the literature. Steggerda's (1940) studies cover many climatic regions, but no two groups had similar genetic and cultural backgrounds. The numerous growth studies within the United States are confined to the north temperate areas and so cannot be used to determine the effects of climate on growth.

In summary, it appears that the characteristics which determine heat tolerance may be divided into several categories depending upon the genetic control. The major mechanisms by which man adapts to the heat are clearly and almost completely determined by genes. Among these mechanisms vasodilation, sweating and acclimatization are the most rigidly inherited. This is not to say that they are not subject to environmental forces because even the most entrenched characteristic is subject to environmental modification. Skin color as it affects heat tolerance is primarily inherited, although there is some environmental modification through tanning. Finally there are the numerous aspects of body composition and form which help determine the human adult's ability to remain in thermal equilibrium when exposed to heat. The fundamental development of these characteristics must be genetically directed, but it is known that a number of nutritional, climatic, traumatic, and infectious agents can drastically alter their phenotypic expression.

CONFORMANCE OF WORLD POPULATIONS TO THEORETICAL MODEL FOR DESERT HEAT TOLERANCE

Having developed a model for desert heat tolerance and investigated its genetic and environmental basis, we may now survey world populations to see how closely they conform. Theoretically, populations living in the desert should vary morphologically in the direction of the model. However, cultural factors might easily intervene to prevent adaptation to climate. For example, certain North African groups highly prize fat women and in this case the value system of the culture tends to inhibit the action of the climatic selection factors. There may also be other physical environmental factors which are more significant for survival than heat strain so that the morphological adaptation to climate is not found. As an example, fat can again be cited. In groups where the food supply is intermittent it may be more important to store energy in the form of subcutaneous fat than it is to have a slightly higher level of heat tolerance.

Considering all the potential modifying forces, one would not, in practice, expect all desert populations to conform perfectly to a model for heat tolerance, but if the model is valid, they should exhibit a general tendency in this direction.

Hot deserts of the world

To compare the theoretical model with the actual populations living in hot deserts we must first establish where the hot desert areas are located

in the world. The term "hot desert" is a somewhat arbitrary term which has been used in this study to designate world areas which are very arid and quite hot for part of the year. The physiologic responses that have been studied relate primarily to the dry and wet bulb temperatures; the type of terrain and vegetation are of secondary importance. However, in areas of high temperature and low humidity, desert terrain is usually encountered. The accepted desert areas may be used with the added limitation of high temperature. Figure 1 shows the best agreement on the extent of world deserts. This composite map was prepared by Francis Ramaley as part of a special report of the Research and Development Branch Office of the Quartermaster General (1952). As this report is not generally available, the following excerpt is included to describe the classification method.

> World deserts have been mapped by using various physical elements, such as landform types and systematic classifications of climate, soils and vegetation. In order to determine the geographical location and distribution of world deserts, several map sources based on each of these criteria were studied and compared. Seventeen such maps representing a typical cross section of criteria, are included in this report. The distribution of world deserts as shown by these maps varies according to the methods, type of criteria, and amount of environmental data used by each author. Differences between maps using similar criteria can be attributed to the amount and completeness of source data used in compiling each separate map. Unfortunately, most such maps are small scale and depend upon liberal interpolation because of gaps in the data used or available. Furthermore, the coincidence between specific climatic and terrain conditions often ascribed to the desert is frequently found only in the more extreme environments. Broad transitional areas representing modifications of these physical conditions present the major problem in delimitation.

Using the composite desert areas as the most valid delineation of true deserts, world maps showing mean July and January temperatures were used to sort out the hot deserts. While means are not necessarily the most valid temperature measurements for describing the heat stress level of a particular desert, in a gross world survey the averages conform adequately to other temperature measurements. The areas of highest monthly temperature are found in Southwestern United States, North Africa, Southwestern Asia and Northwest Australia. Jones' map of Desert Climates is the best available classification of deserts for the purpose of this study (Jones and Wittlesey, 1928). His classification, "low latitude desert," conforms to what has been called "hot desert" in this study.

Many more areas have hot climates that periodically approximate desert humidities. For example, much of India has a spring climate that can be classified as hot and dry. However, the long summer period of tropical monsoon rains prevents the area from being classified as desert. Seasonal deserts cannot be utilized in this study because man is subjected to tropical heat stress in these areas as well as to desert heat stress. It cannot be concluded that these forces are similar, and, in fact, they might conceivably lead to quite different forms of adaptation.

Still other areas have not been classified as deserts by Jones because of atypical terrain. Certain of these places can be included in this study since

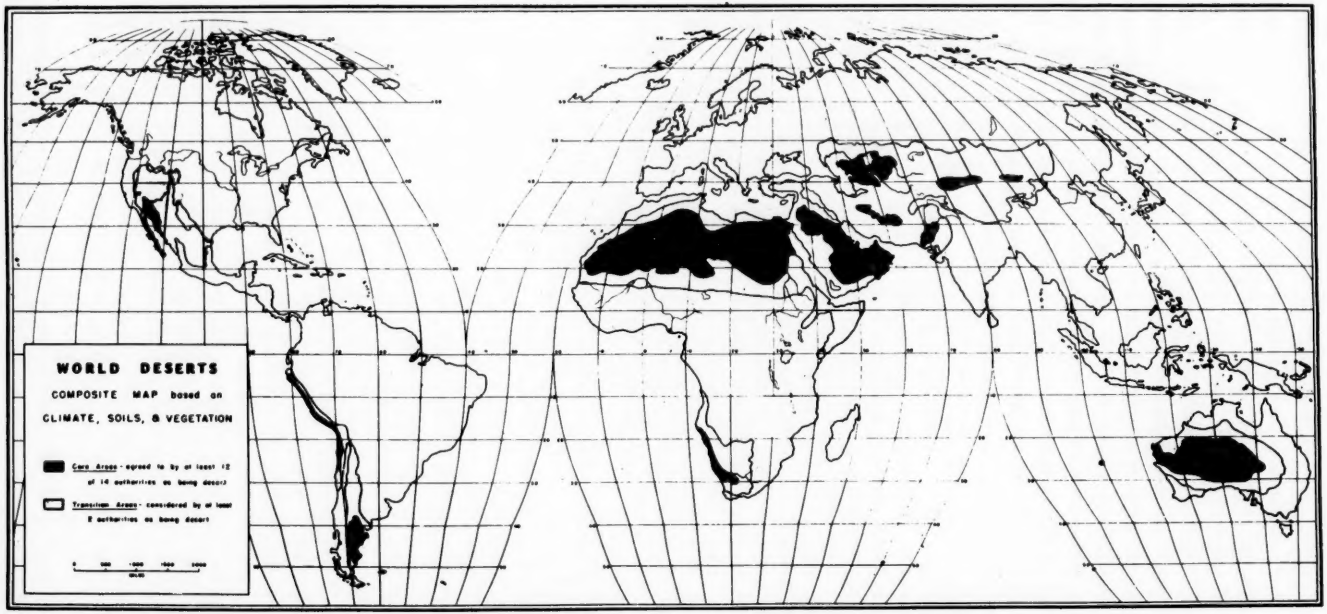

FIGURE 1. World deserts—composite map based on climate, soils, and vegetation. (Map prepared by Francis Ramaley as part of a special report of the Research and Development Branch, Office of The Quartermaster General, 1952).

it deals only with temperature and moisture factors. A recent analysis of the Middle East climate compared the temperatures and humidities (Analogs of Yuma Climate, 1954) where most of the model information was developed. On the basis of this comparison, a much wider and important area may be included. This includes the Tigris-Euphrates Valley. Previous classification by Jones made the Indus River and Nile River areas desert. Thus, considering recent climatic conditions, three important loci of early "civilization" had hot desert climates even though atypical terrain.

Model components

The relationship between the model characteristics and actual population measurements would ideally consist of a comparison of desert populations and those surrounding them. Unfortunately, not enough information about these populations is known for such a comparison and consequently a survey of all the known populations provides the maximum data which can be amassed on the subject.

Skin color

The skin colors of desert populations have not been accurately measured, and we must rely on subjective judgments for estimates of melanin content. On this basis the desert groups appear to conform quite well to the model criteria of brunette skin. The darkest desert people are probably the Negroes who inhabit the southern fringes of the Sahara or perhaps some of the Australian groups; the lightest people are some of the North African Berber groups. Between these extremes are such groups as the Bushmen of the Kalahari, the Papago of the South Western United States desert, and the other Mediterraneans of the Sahara and Near East areas. Thus, as a generalization, we may say that hot desert populations are intermediate in skin melanin content.

Body fat

Three methods have been used for assessing fat. The first of these is the direct measuring of skinfolds, body density, or x-rays. The second is the observational or somatoscopic technique, and the third is the relative weight criterion. Direct measurement methods are recent and only a few populations have been sampled to date. Fat data derived from specific gravity and x-ray methods are available only for North European and North American populations. Skinfold measurements are simpler and, therefore, larger samples exist. The material published to date is summarized in table 1. These skinfold measurements were made with differing caliper tensions rendering the measurements not completely compatible. However, it appears that the Northern and White populations are the fattest. This may be purely a matter of nutrition, but observation using the somatoscopic technique indicates that most hot climate populations have less fat than cold climate groups. Within the somatotyping system, which conforms quite well to direct fat measurement (Dupertuis et al., 1950), North American Whites

TABLE 1

SKINFOLD MEASUREMENTS FOR VARIOUS POPULATIONS

Group	Source	N	Age	Caliper pressure g/sq. mm	Skinfolds (mm)	
					Arm	Back
U. S. White Soldiers	(Newman '56)	2017	20.7	5	11.4	13.6
U. S. Negro Soldiers	(Newman '56)	361	20.8	5	8.2	12.2
U. S. Students	(Brozek & Keys '51)	133	20.3	35	10.9	14.3
U. S. Businessmen	(Brozek & Keys '51)	122	49.0	35	14.4	19.9
Spanish Laborers	(Keys et al. '54)	22	26.0	10	7.3	9.1
Spanish Professional	(Keys et al. '54)	35	26.1	10	14.1	...
Chinese Soldiers	(Crowley et al. '56)	1049	26.8	5	4.2	7.9

are fatter than the Japanese (Kraus, 1951), who are in turn still fatter than Native East Africans (Danby, 1953). It could still be argued that this is nutrition. However, Cullumbine (1953) has shown by direct fat measurement that the Ceylonese are quite low in fat despite an adequate diet. Henckel (1950) reports that the Indians of Southern Chile who had a simple hunting and gathering culture predominated in the "pyknic" body form. Thus, fat groups are found in cold climates even when the diet might be judged as poor. The extremely dubious method of inspecting available photographs also seems to support a cold climate distribution of fat peoples, while the hot desert populations such as the Mediterraneans, Bushmen, Hottentots, Nilotics, and Australians all appear very slender (Coon, Garn and Birdsell, 1950). There are, of course, exceptions. Gabel (1949) observed that the Papago of the U. S. Southwestern desert were quite fat but considering all of the cultural and environmental forces which might modify a group in this direction, the few exceptions to the model are not at all surprising.

The third method of measuring fat by relative body weight was rejected for this study. Within a limited racial and cultural group this criterion has a relationship to body fat, but in comparing the linear Nilotic Negro with the short-legged Eskimo it is impossible to see how relative weight in any manner reflects body fat.

Body mass and surface area

Recent anthropological interest in the relationship between climate and body form has concentrated on the body size and surface area in relationship to climatic indices (Roberts, 1953; Schreider, 1950 and 1951; Schwidetzky, 1952; and Newman, 1955). The index of surface area over weight is presumably a double-edged sword because high mass per surface area helps heat conservation, while high surface area per unit mass helps the loss of heat. Scholander (1955) recently criticized the selective value of minor changes in this ratio for adaptation to cold. His criticism, while pertinent, is based on the gross adaptations exhibited by animals and as pointed out by Marshall and Newman (1956) even slight variations in adaptations may be important to men living in critical climatic areas.

Certain very important limitations arise in any effort to study population differences in surface area. This characteristic is very difficult to measure directly and, consequently, almost all surface areas reported are estimated by means of the Du Bois (1936) formula using stature and weight:

$$(\text{Surface Area} = \text{Weight}^{0.425} \times \text{Height}^{0.725} \times 71.84).$$

These comparisons of weight to surface area are, therefore, merely some form of a height-weight ratio. For this reason in the present study we have dealt with the direct measurements. Although surface area over weight is physiologically a more rational index than height over weight, the lack of direct measurements of surface area makes height over weight a more valid ratio. Appendix A shows the height, weight and height/weight distributions for world populations. Beside the simple height/weight ratio, these body characteristics were combined in a calculated index called "theoretical sweat loss." Experimental studies (Baker, 1955) indicated that sweat loss under specific hot desert conditions could be predicted with reasonable accuracy from height and weight. Therefore, the regression equation derived from these experiments was used to calculate a theoretical sweat loss (sweat loss in liters/hour) for world populations in order to indicate the potential significance of these measurements to desert heat tolerance. The use of a regression based on a small group of White soldiers for prediction of the sweat loss of many world populations is obviously a very speculative procedure. The prediction is made without regard to racial factors or local environmental conditions, but from the study of American Whites and Negroes it appears that racial differences in sweat loss are mostly referable to body composition differences (Baker, in press). Even if race does not strongly affect sweat loss, prediction for a very large sample from such a small sample means that the slope of the regression may be many degrees off the true slope. Only a few of the groups which have been considered will ever by exposed to conditions similar to those for which sweat loss has been predicted, and even in these groups the differing acclimatization and environmental backgrounds would probably cause their sweat loss to vary somewhat from that predicted. The prediction is, therefore, not to be considered a practical tool. Instead, the theoretical sweat loss was calculated as a more rational expression of height and weight in relationship to the potential heat strain of various world groups.

In figure 2 the world distribution of theoretical sweat losses has been plotted. There is a world regression in which, with some variation, the predicted sweat loss becomes lower as the climate becomes hotter. Within certain racial groups the relationship between theoretical sweat loss and climate is even more definite. The highest sweat loss among Whites is found in the North Temperate areas; in particular, high theoretical sweat loss is found among the Finns, Irish, Icelanders, U. S. soldiers, Parisians, and French soldiers. The intermediate sweat losses are found in Central and Southern European groups and the lowest values occur among the Mediterranean groups in Arabia and North Africa.

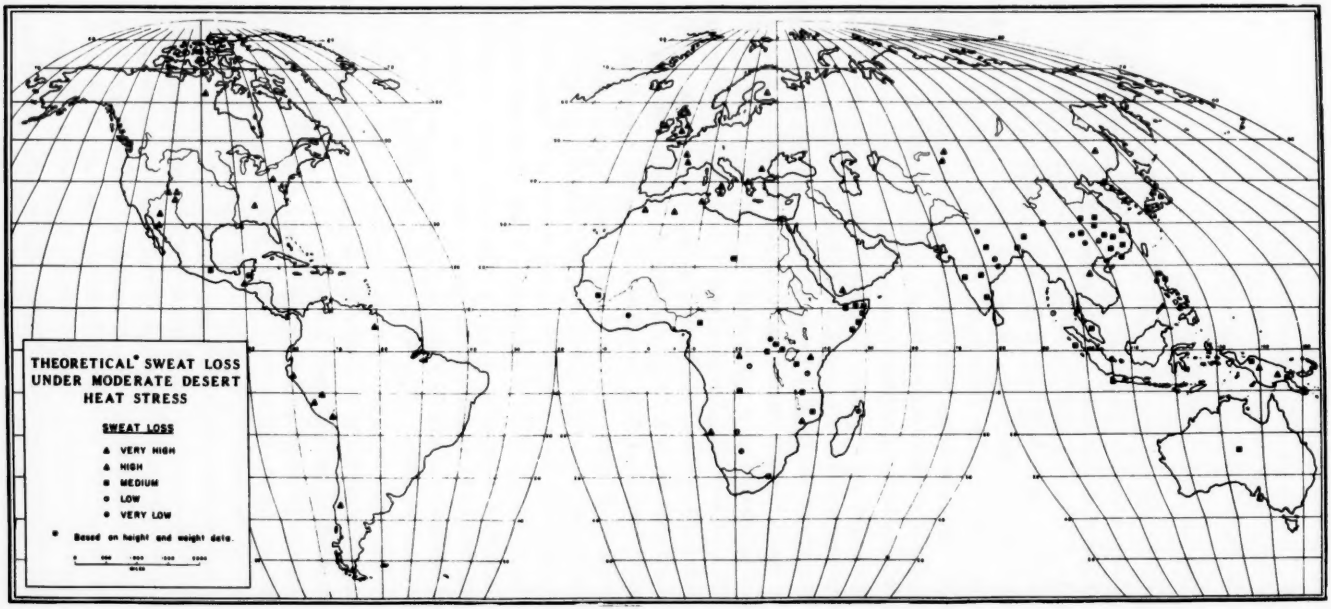

FIGURE 2. Theoretical sweat loss—based on the relationship found between body weight, stature and sweat loss for a group of U. S. soldiers walking in a hot desert.

Eastern Hemisphere Mongoloid groups are distributed from very cold to very hot climates and these groups show a very close correspondence between theoretical sweat loss and climate. Even within the subgroups the relationship is very strong. Four Korean samples representing different provinces were found. Theoretical sweat loss was lower in the Southern provinces than in the Northern ones. In China where many samples were available there was a very decided regression of theoretical sweat loss on climate even though a few samples are out of line. Material on Western Hemisphere Mongoloids is sparse and shows little relationship. Within the New World population, settlement was quite recent and in many of the cases cited a movement of a few miles would drastically alter the climatic conditions encountered.

Theoretical sweat losses in African Negroes show a general relationship to temperature in that the highest sweat losses are associated with peoples dwelling in the temperate savannas and the lowest with the smaller groups of the tropical forests and deserts. In Africa the climatic differences encountered are primarily associated with altitude and it is, at this time, impossible to differentiate the biological responses which are associated with temperature from those associated with altitude.

The South Asian non-Mongoloids and Oceanic non-Mongoloids were merely geographic categories in which no genetic affiliation was intended. There are several population aggregates in which insufficient groups were available for within-population analysis. These population groups fit into the world relationship of theoretical sweat loss to climate but cannot be investigated for within-group variation.

Inspection of both the worldwide and within-group distribution of theoretical sweat losses shows that in cold climates theoretical sweat losses are always high and in hot climates are usually low. However, in the intermediate or neutral climates population groups may vary to the extremes in sweat loss. This strongly suggests that extreme climates act as selective forces. Thus, biological characteristics show broad between-group variation in populations dwelling in non-selective neutral environments, but only populations which have the advantageous extreme survive in the climatologically rigorous zones.

Desert populations do not have a mean theoretical sweat loss significantly different from other populations living in hot areas, but they do show more variation. For example, Bushmen, Australians, and Papagos encompass a range in body size equal to any in the world. The large range in body size and theoretical sweat losses is compatible with the experimental findings, because for desert dwellers large size is not an important handicap in thermal regulation provided adequate drinking water is available. However, from the experimental evidence it also appeared that individuals with low weight-per-unit stature showed lower strain as indicated by sweat loss. This seeming paradox can be explained, if it is postulated that there is a species-wide decrease in surface area per unit weight as weight increases and that this relationship is not connected to desert heat tolerance.

However, individual or group departures from this species-wide decrease do affect heat tolerance. More simply stated, there is a known high positive correlation between the weight-per-unit stature and weight. By the nature of the human form large men normally have a lower surface area or stature per unit of weight. Thus, large men may be subject to strong negative selective forces in hot wet areas where all sweat is not evaporated because of high humidity, but this normal regression does not affect desert heat tolerance. On the other hand, individuals who depart from the normal regression by having low or high surface areas for a given weight do show accompanying lower or higher desert heat tolerance. If the preceding speculation is acceptable, then the findings based on the calculations of theoretical sweat loss would be reasonable, in that a selective force for small men is indicated for hot wet areas but not for dry ones. The use of height and weight as indicators of biological desert heat stress resistance would require that we first approximate the normal parameter for the weight to weight-per-unit-stature regression, a calculation for which data on world populations is not at present adequate.

SUMMARY AND CONCLUSIONS

Man, who first evolved as a tropical animal, has spread over most of the climates of the world. This has been made possible by his invention of cultural aids. However, in many cases he has extended his habitat into alien climatic zones without important aids to modify the forces of the temperature regime. This has led several anthropologists to conclude that man has probably adapted to a climate as have other mammals. The evidence for this conclusion has rested on the relationship between morphological characteristics and climate. However, other environmental factors vary with climate so that it is difficult to be sure which environmental isolates are significant for adaptation. In this paper an experimentally derived model was developed for resistance to desert temperature stress. By surveying the literature, a number of morphological characteristics were selected which have been demonstrated to affect man's ability to withstand the thermal stress which is unique to hot deserts. Using these criteria, it was shown that a linear, acclimatized man with brunette skin and low body fat would be the best suited individual for work under hot desert conditions. These morphological attributes were then reviewed to indicate the genetic and environmental forces which determine their adult phenotypic expression. It was found that a very significant fraction of the phenotypic appearance of these attributes is determined by genetic structure. Therefore, if the hot desert populations conform to the model, either selective migration or genetic adaptation must have occurred.

It must be recognized that, besides climate, other natural environmental forces and cultural forces act to form the phenotypic expression of these body characteristics. Many of these forces counteract climatic selection and thus an imperfect relationship between the theoretical model and the true desert populations is to be expected. However, a survey of the model characteristics in world populations indicated that, although we have scant

data, the available material on desert populations conforms fairly well to the model. From this conformance, two conclusions may be drawn: first, that the model contains valid morphological characteristics for desert heat tolerance; and second, that man has to some extent genetically adapted to the climatic conditions found in a hot desert.

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APPENDIX A

WORLD DISTRIBUTION OF WEIGHT, HEIGHT AND THEORETICAL SWEAT LOSS*

Group	Sample size	Weight kg.	Stature cm.	Stature / Weight	Theoretical sweat loss per hour kg.
Whites					
Finland	many	70.0	171.0	2.44	1.193
U. S. Army	85,774	70.2	173.9	2.48	1.176
Bulgars	121	67.1	167.2	2.49	1.169
Ballymoney Irish	111	68.2	171.9	2.52	1.155
Ballycastle Irish	185	68.5	172.8	2.52	1.154
Parisians	72	67.0	168.8	2.52	1.155
French Soldiers	75	65.4	166.2	2.54	1.145
Iceland	652	68.1	173.6	2.55	1.141
Ballymena Irish	157	67.3	171.7	2.55	1.140
Greek	80	64.4	164.8	2.56	1.137
English Prisoners	150	65.1	166.6	2.56	1.137
East Coast Irish	50	66.3	170.4	2.57	1.131
Paris	2,619	67.0	172.5	2.57	1.129
England	3,000	64.5	166.3	2.58	1.128
English Students (Oxford)	433	68.7	178.2	2.59	1.121
Italian Soldiers (Sicily)	107	65.0	169.1	2.60	1.117
Moroccans	132	63.8	168.9	2.65	1.097
Lima Soldiers	15	58.0	158.0	2.72	1.064
Cornwall England	many	63.0	171.7	2.72	1.064
Sicily	29	59.2	162.4	2.74	1.057
Southeast England	many	63.0	173.0	2.75	1.056
Edinburgh	many	61.8	170.4	2.76	1.051
London	many	62.2	172.2	2.77	1.046
Arabs (Yemen)	21	58.6	162.6	2.77	1.044
Tunisians	53	62.3	173.4	2.78	1.041
Glasgow	many	60.5	169.4	2.80	1.034
Staffordshire	many	60.8	170.9	2.81	1.030
Berbers (Giado)	19	59.5	169.8	2.85	1.014
Daonad (Fezzan)	25	54.4	166.4	3.06	.942
African Negroids					
Bakiga	70	64.5	168.4	2.61	1.113
Yambasa	248	62.0	169.0	2.72	1.064
Masai	76	61.3	172.0	2.80	1.032
Dzimon	83	57.7	163.4	2.83	1.022
Nhungnes (Mozambique)	120	59.3	168.0	2.83	1.021
Warega	100	57.2	162.1	2.83	1.021
Djem	100	56.6	162.9	2.88	1.005
Darod (Somalie)	124	59.3	172.2	2.90	.995
Kirdi	881	57.3	166.5	2.90	.994
Bahutu	400	57.1	166.5	2.92	.991
Gobaouin (Somalie)	50	57.5	168.4	2.93	.986
West Africa	28	57.0	167.3	2.94	.984
Rahanaouin (Somalie)	117	57.6	169.4	2.94	.982
Antumbas (Mozambique)	28	55.4	164.9	2.98	.970
Dir (Somalie)	47	57.5	172.9	3.01	.959

*Height and weight data in this table were obtained from the following sources: Cadbury, 1924; Gabel, 1949; Newman and White, 1951; Roberts, 1953; Schreider, 1950 and 1951; Seltzer, 1936; and Wilson, 1950.

APPENDIX A (*continued*)

Group	Sample size	Weight kg.	Stature cm.	Stature / Weight	Theoretical sweat loss per hour kg.
African Negroids (continued)					
Baya	412	53.9	163.0	3.02	.954
Badjone	200	55.0	166.6	3.03	.952
Bashi	108	53.5	163.9	3.06	.940
Haoniya (Somalie)	87	56.8	174.4	3.07	.938
Batutsi	296	57.0	176.0	3.09	.933
Nyaturu	50	52.2	165.4	3.17	.908
Kikuyu	536	51.9	164.5	3.17	.907
Batwa	113	48.7	155.3	3.19	.901
Jmbo	28	49.5	161.3	3.26	.881
Sandawe	100	49.4	164.6	3.33	.860
Pygmy	147	39.9	142.2	3.56	.801
Akka	115	40.0	144.4	3.61	.790
Efe	386	39.8	143.8	3.61	.789
Gagnon	24	42.6	159.3	3.74	.761
Bushmen	88	40.4	155.8	3.86	.736
Kung (Kalahari)	32	40.4	156.8	3.88	.731
Eastern Hemisphere Mongoloids					
Kazak	30	69.7	163.1	2.34	1.248
Orochee	93	59.5	155.0	2.60	1.116
North China	?	61.0	168.0	2.75	1.052
Korea	594	59.2	163.2	2.76	1.051
Kirghiz	40	59.7	165.3	2.77	1.046
Indochinese (Tonkin)	99	57.2	159.9	2.80	1.036
Korea (Pjonjan)	45	56.8	163.0	2.87	1.008
Korea (Hwanhai)	22	55.6	160.3	2.88	1.003
Korea (Chung Chong)	27	55.8	161.3	2.89	1.000
Korea (Kyong Kwi)	354	55.5	161.1	2.90	.996
Kwangtung	203	55.0	160.7	2.92	.989
Chihli	261	57.3	168.9	2.95	.980
Pekin	83	56.9	168.4	2.96	.975
Central China	328	54.7	163.0	2.98	.968
Kiagei	700	55.4	166.1	3.00	.962
Malay	50	55.5	166.4	3.00	.962
Japanese	774	53.0	160.9	3.04	.950
Hokle	117	53.6	162.7	3.04	.950
Mentawei	202	51.5	156.5	3.04	.949
Central China	351	54.0	165.0	3.06	.943
South China		54.0	165.0	3.06	.943
Banjerese	35	51.3	157.0	3.06	.942
Filipino	88	53.0	163.0	3.08	.937
Sundanese	237	51.9	159.8	3.08	.936
Chekiang	259	52.8	162.8	3.08	.934
Annamites	many	51.3	158.7	3.09	.931
Naga	33	51.5	160.3	3.11	.925
Japanese	42	51.9	161.9	3.12	.923
South China	30	52.3	163.4	3.12	.921
North China	23	50.9	159.0	3.12	.921
Hongkong	202	52.2	166.2	3.18	.903
Szechuan	54	51.7	165.0	3.19	.901
Javanese	57	51.2	164.0	3.20	.897
Hunan	267	50.1	161.5	3.22	.891

APPENDIX A (*continued*)

Group	Sample size	Weight kg.	Stature cm.	$\frac{\text{Stature}}{\text{Weight}}$	Theoretical sweat loss per hour kg.
Eastern Hemisphere Mongoloids (continued)					
Miao	24	46.4	154.0	3.32	.864
Szechuan	70	45.8	166.1	3.63	.786
Western Hemisphere Mongoloids					
Papago	219	71.4	168.8	2.36	1.235
Mapuche	31	66.8	163.3	2.44	1.192
Santa Lucia	16	63.0	159.0	2.52	1.153
Choctaw	33	67.8	171.4	2.53	1.151
Eskimo	190	62.9	161.2	2.56	1.135
Oroya	18	62.7	162.0	2.58	1.125
Yaqui	100	64.0	166.7	2.60	1.116
Arequipa	44	61.0	160.0	2.62	1.107
Hopi	276	60.8	161.1	2.65	1.096
Piura	23	60.6	160.7	2.65	1.095
Navaho	125	62.7	169.6	2.70	1.072
Maya Zuiche	30	57.6	159.3	2.76	1.048
Peru	many	56.2	159.0	2.83	1.023
Surinam	27	56.5	160.1	2.83	1.021
Zuni	348	56.3	161.4	2.87	1.009
Maya	156	53.5	156.8	2.93	.986
Otomis (Mexico)	107	53.2	157.6	2.96	.975
Oceanic non-Mongoloids					
Hawaii	60	77.3	171.3	2.22	1.321
Maori	384	74.5	170.6	2.29	1.277
Massawa	49	58.7	160.5	2.74	1.060
Jabim	26	56.4	161.0	2.85	1.013
Ana	29	54.3	157.1	2.89	.999
Mira	20	53.1	161.5	3.04	.948
Central Tribes (Australia)	47	55.3	169.1	3.06	.942
Aeta (Bataan)	36	41.5	147.7	3.56	.802
Aeta (Zambales)	46	40.5	148.1	3.66	.779
South Asian non-Mongoloids					
Mahratta	162	55.7	163.8	2.94	.982
Brahmin	100	55.5	163.8	2.95	.978
Mande	23	53.6	158.8	2.96	.974
Bombay	84	54.6	167.4	3.06	.940
Hyderabad	32	54.2	169.3	3.12	.921
Madras	61	53.1	167.0	3.14	.915
Bengal	1,193	52.7	165.8	3.15	.915
Senoi	78	47.6	155.5	3.27	.879
Andamanese	40	44.7	147.8	3.31	.867
Santal	313	45.0	159.3	3.54	.807
Semang	26	41.4	153.7	3.71	.767
Malpaharia	60	41.6	156.3	3.76	.757
Sauriakaharia	69	41.4	156.2	3.77	.753

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DEVELOPMENT OF BALANCED POLYMORPHISM IN LABORATORY POPULATIONS OF *DROSOPHILA MELANOGASTER*

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INTRODUCTION

Balanced polymorphism is characteristic of many natural populations. When samples of such polymorphic populations are removed to the laboratory and reared there, the polymorphism frequently persists, sometimes indefinitely (for example, Wright and Dobzhansky, 1946; Dobzhansky, 1948; da Cunha, 1949; Spiess, 1950; Levitan, 1951). The cases involving inversion polymorphism have been most frequently interpreted as being due to the persistent heterotic properties of chromosome segments which have been coadapted by natural selection acting in natural populations.

A number of instances are known, however, in which a heterotic condition has arisen and has been maintained in an experimental laboratory population in apparently stable equilibrium despite the fact that the hereditary elements involved in the polymorphism came from diverse geographical areas or were so unrelated that prior coadaptation could be excluded as a possibility (Tessier, 1947b; Reed and Reed, 1948; Dobzhansky and Pavlovsky, 1953).

For these cases in which a new balanced condition has developed, two explanations, which are not mutually exclusive, seem possible. First, coadaptation (= relational balance) could result from the action of natural selection in the laboratory population (Dobzhansky and Pavlovsky, 1953; Tebb and Thoday, 1954). Secondly, heterosis without prior coadaptation, or heterozygosity *per se* for particular loci or chromosome sections may function to provide a basis for the initiation of balanced polymorphism. This paper presents evidence that under certain circumstances simple heterozygosity may indeed contribute to a newly-arisen balanced polymorphism.

MATERIAL AND METHODS

A stock of the third chromosome recessives sepia (*se*) spineless (*ss*) and rough (*ro*) of *Drosophila melanogaster* (Cold Spring Harbor No. 260a; see DIS-28: p. 28) was used as a base population. Into it was introduced a single haploid set of wild type autosomes derived from a single wild male caught in University City, Missouri. The introduction was accomplished by crossing the wild male to a *se ss ro* female and selecting single sibling F_1

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males for introduction into the populations. Each of the two replicate initial populations (table 1) was composed of 50 flies, 25 females and 24 males homozygous for *se ss ro* and one wild type male heterozygous for *se ss ro*, as described above. Thus the beginning frequency of individuals carrying a homozygous recessive genotype was 98 per cent (gene frequency of either *se* or *ss* or *ro* = 99 per cent). Counts were made of the populations every two days from the 29th through the 51st days and thereafter at less regular intervals (table 1).

A type of experimental vial population similar to that described by Buzzati-Traverso (1955) was used. The populations were initiated in standard 25 × 95 mm shell vials. The parent population was transferred to a fresh vial every two days thereafter. As they hatched, all offspring were added to the parent population every two days, at the time of transfer. Each vial contained approximately 10 cc of cornmeal-Karo-agar medium yeasted with three drops of a suspension made by adding 10 drops of water to 200 mgs of Fleishmann's dry yeast. A small piece of Kleenex tissue was added to absorb the excess moisture. No further food was provided for either adults or larvae.

Under these conditions, the minimum time from egg to adult is about 13 days; this generation time has been used in table 1. Each vial was discarded after having been held for 20 days, whether or not all flies had emerged. The experiments were carried out at 25 ± 2°C.

OBSERVATIONS

At various intervals after the initiation of the experiment in duplicate (populations A and B) on February 25, 1956, each entire adult population was lightly etherized and all or part of it was counted, after which the individuals were returned to the population vial. The results of these counts are given in table 1. Although at each count the flies were recorded as wild type, *se ss ro*, or any of the six crossover types, the results are given here in per cent of the total counted having each of the three homozygous mutant genotypes.

Both populations were kept for eleven generations in vial populations after which they were placed in ordinary stock bottles and maintained on a routine schedule of one weekly change. Population B was discarded in November, 1956, after 20 generations.

In May, 1957, two replicates of population A (A 1 and A 2, table 1) were returned to experimental vial populations; A 1 was replaced in stock bottles and A 2 discarded in August, 1957. A 1 has been maintained in stock bottles since that time, to date (August, 1958).

In both populations all three homozygous mutant genotypes declined catastrophically and within three generations had been reduced to levels between 4 and 10 per cent. Although there are apparently significant oscillations after this time the systematic declines in both *ro/ro* and *se/se* were arrested after about three generations (table 1). In 1957 and 1958, the *ro/ro*

TABLE 1

EXPERIMENTAL BALANCED POLYMORPHISM IN *DROSOPHILA MELANOGASTER*. THE MUTANT STOCK *se ss ro* WAS INOCULATED WITH A HAPLOID SET OF AUTOSOMES DERIVED FROM A SINGLE WILD MALE. V – POPULATION WAS IN EXPERIMENTAL VIAL POPULATIONS; $ – POPULATION HAD BEEN RETURNED TO STANDARD HALF-PINT STOCK BOTTLES.

Date	Time from beginning		Population type	Number of individuals counted		Per cent of individuals showing the mutant phenotype					
						ro/ro		*se/se*		*ss/ss*	
	Days	Generations		Pop. A	Pop. B	Pop. A	Pop. B	Pop. A	Pop. B	Pop. A	Pop. B
1956											
Feb. 25	0	0	V	50	50	98.0	98.0	98.0	98.0	98.0	98.0
Mar. 22	26	2	V	277	213	52.0	49.3	52.0	49.3	52.0	49.3
Mar. 24	28	2	V	214	260	37.9	56.3	37.9	56.7	37.9	56.7
Mar. 26	30	2	V	327	264	44.9	48.6	44.6	49.8	44.6	49.0
Mar. 28	32	2	V	333	260	37.9	40.4	37.6	40.8	37.6	41.2
Mar. 30	34	2	V	195	257	26.1	26.1	26.1	26.9	25.6	27.3
Apr. 1	36	2	V	210	284	20.9	25.0	20.9	25.7	20.0	26.5
Apr. 3	38	3	V	254	270	20.1	20.0	21.7	20.0	20.1	20.4
Apr. 5	40	3	V	278	303	13.7	14.1	14.8	12.6	12.6	12.9
Apr. 7	42	3	V	343	313	10.2	7.0	10.5	6.0	7.9	8.0
Apr. 9	44	3	V	301	255	7.7	5.5	7.3	3.6	4.7	4.8
Apr. 11	46	3	V	385	234	9.6	7.7	7.3	3.9	4.9	6.1
Apr. 13	48	3	V	423	...	8.3	...	7.8	...	4.0	...
Apr. 15	50	3	V	326	...	9.7	...	7.3	...	3.3	...
Apr. 19	54	4	V	250	385	10.4	14.3	4.8	10.9	2.4	9.7
May 3	68	5	V	250	216	11.2	14.3	8.7	4.6	5.2	2.8
May 13	78	6	V	192	217	12.5	14.3	11.5	10.7	5.2	4.2
May 17	82	6	V	238	250	15.9	14.0	8.3	8.0	6.7	3.6
June 18	118	9	V	335	430	16.1	18.4	6.3	8.1	1.8	5.1
July 13	143	11	V	562	583	12.3	14.4	11.9	9.8	2.1	5.0
Nov. 1	254	19	$	249	338	16.1	12.4	11.2	0.9	5.6	3.8
					finis		finis		finis		finis
				Pop. A1	Pop. A2	Pop. A1	Pop. A2	Pop. A1	Pop. A2	Pop. A1	Pop. A2
1957											
May 7 & 9	440	34	V	182	305	18.2	13.4	3.3	0.0	1.2	1.3
May 11 & 13	444	34	V	231	210	19.5	11.4	2.6	0.0	0.0	1.9
May 15 & 17	448	35	V	185	284	21.1	9.6	2.2	0.4	0.0	1.5
May 21 & 23	454	35	V	174	207	20.1	9.7	2.8	0.5	0.0	0.0
May 25 & 27	458	35	V	248	237	22.2	14.3	3.2	1.3	1.6	1.3
May 29	462	35	V	...	210	...	11.4	...	2.9	...	3.4
May 31	464	35	V	...	222	...	11.8	...	1.9	...	1.9
June 6	470	36	V	221		25.4		6.1		6.8	
Aug. 8	533	42	V	190	finis	16.8	finis	3.7	finis	0.5	finis
1958											
June 25	854	67	$	481		14.5		7.3		0.8	
Aug. 6	896	69	$	406		8.9		16.0		1.5	

genotype had a mean frequency of about 16 per cent. The minimal gene frequency of *ro* may thus be roughly estimated as the square root of this, or 40 per cent. The *se/se* genotype averaged about 4 per cent in 1957-1958; the gene frequency of *se* may be estimated at 20 per cent. The *ss/ss* genotype, after declining initially to about 4 per cent has since declined further; it showed a mean level of 1.5 per cent in 1957-1958. This latter figure indicates a minimal gene frequency of about 12 per cent for this gene.

DISCUSSION

The basic result of the experiment seems clear. The introduction of one haploid set of autosomes, including of course a single wild type allele of each of the mutant genes *se*, *ss* and *ro*, has not been followed by elimination of either the mutant or the wild type alleles. Rather, it is clear, in the cases of the genes *ro* and *se*, that balanced equilibria were quickly established and have been maintained for more than 65 generations thereafter. In the case of the third gene, *ss*, several declines in frequency have been observed; nevertheless even this gene remains in the population at a frequency of about 12 per cent.

Tessier (1943, 1947 a) described an experimental population of *D. melanogaster* in which an apparently newly-mutated allele of sepia (se^{42}) arose. This gene remained in this population, and a replicate of it, for more than two years. At the termination of the experiments, se^{42} showed a frequency of 14.8 per cent and 17.6 per cent respectively. Similar stable equilibria have been observed repeatedly for the gene ebony (L'Héritier and Tessier, 1937; Tessier, 1947 b; Kalmus, 1945). Tessier (1942) observed an apparently stable equilibrium for Curly; and Reed and Reed (1948) and Merrell and Underhill (1956) have demonstrated comparable equilibria for various sex-linked genic and chromosomal conditions. That spineless and aristopedia can also coexist in balanced condition is suggested by the data of Kerr and Wright (1954). Our observations on *ro* and *se* are in accordance with the above cases.

In the case of *ss* in our experiments and in some other cases in the literature (for example, Bar—L'Héritier and Tessier, 1937; yellow—Merrell and Underhill, 1956) the levels reached by the mutant gene are so low that a decision cannot be made as to whether a true balanced condition has been reached at a low gene frequency level or whether the polymorphism is transient, with a gradual continuing elimination of the mutant gene. Balanced equilibria are therefore better observed in genes such as *se*, *ro* or ebony which tend to stabilize at high frequencies. Equilibrium conditions, however, are by no means universal and some genes are quickly and systematically replaced by their wild alleles. Thus, Merrell and Underhill (1956), who infected populations of the autosomal recessives vestigial and glass with single wild type males, observed 19 eliminations in 20 experiments. Buzzati-Traverso (1955) observed the elimination of white and Bar from four replicates and Reed and Reed (1950) the elimination of white from three

replicates. In all these cases, however, more than a single wild type allele was introduced to compete with the mutant; the possibility that balance could have arisen between two different but phenotypically indistinguishable wild type alleles should not be overlooked.

The balanced condition observed in these experiments is evidently due to heterosis, such that heterozygotes at the loci concerned are superior in fitness, under the conditions of the experiment, to either of the homozygotes. The speed with which the basic levels of gene frequency are attained is prodigious in our experiments (about three generations) and this appears to be also generally true in the other experiments cited above. It would appear, therefore, that the initial establishment of equilibrium can have been little influenced by the development of relational balance in the experimental populations. Such a coadaptive process must rely on extensive polygenic recombination and selection and would therefore require more time to be effective.

The evidence therefore indicates that simple heterosis at certain loci can indeed form a basis for balanced polymorphism and that such loci need not necessarily be exposed to coadaptive background influences for such a heterosis to become established. This conclusion, quite obviously, does not preclude the development of coadaptive heterosis in later generations. In fact, as Tessier (1947b) has suggested, recombinations in the genetic background may indeed be an important factor causing the frequently observed shifts from one gene frequency level to another, a characteristic feature of this type of experiment.

It seems possible, therefore, that both simple and coadaptive heterosis may contribute to fitness (see Dobzhansky, 1955, pp. 7-8). Further efforts are being made (Carson, 1958) to assess the relative roles of these two kinds of heterosis, using the production of biomass as a measure of fitness.

SUMMARY

Introduction of a single set of wild type autosomes into experimental populations of *D. melanogaster* homozygous for sepia, spineless and rough resulted in the quick assumption of a condition in which rough and sepia are balanced in the population at gene frequencies which have not declined progressively thereafter for a period of two and a half years (70 generations). The gene spineless, on the other hand, declined several times to new low levels but has not been eliminated. Its final frequency, about 12 per cent, is sufficiently low that slow elimination cannot be ruled out.

These results are explained by the hypothesis that the heterozygotes, at least for rough and sepia, show superior fitness under the conditions of the experiment. As the condition was established almost immediately, it is likely that simple heterosis at certain loci (or possibly adjacent chromosome sections) functions in the immediate establishment of equilibria without the necessity of prior coadaptation.

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INFLUENCE OF SEED IRRADIATION WITH X-RAYS AND THERMAL NEUTRONS UPON CELL SIZE AND MITOTIC ACTIVITY IN ROOT TIPS OF MAIZE*

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In recent years a number of reports (for example, Caldecott et al., 1952, 1954, 1955; Schmidt and Frolik, 1951; Schwartz, 1954; Schwartz and Bay, 1956; Spencer and Cabanillas, 1956; Yagyu and Morris, 1957) have appeared which deal with the effects of treating seeds with various high energy radiations. In all cases it is reported that seedlings grown from appropriately-irradiated seeds are reduced in stature. This reduction in stature must necessarily result from irradiation-induced decreases in number and/or size of the cells comprising the seedlings. Although some quantitative data relating to irradiation-induced changes in cell size and mitotic activity are available in the literature (Lea, 1955), there is a paucity of this type of information dealing with the seedlings grown from irradiated seeds. This report deals with a study in which cell size and mitotic activity have been measured in tips of roots grown from control and irradiated maize seeds.

MATERIALS AND METHODS

Seeds of the single-cross maize hybrid, L289 × I205, were used in these studies. X-ray and thermal neutron treatments were administered at the Brookhaven National Laboratory, under the supervision of Dr. Seymour Shapiro. The irradiation procedures were similar to those which have been described elsewhere (Haskins and Chapman, 1956).

Thirty-five seeds from each treated lot and from a control lot were immersed for five minutes in a 1 per cent sodium hypochlorite solution, rinsed several times in distilled water, and allowed to germinate at 24°C. in moist vermiculite in the dark for a period of about 65 hours. After this germination period, seedlings were washed free of vermiculite and were sorted according to length of primary root into four groups of seven or eight seedlings for each of the treatments. Following measurements of root length, the terminal 3-mm. portion of each primary root was removed and placed in a fixative solution prepared according to the directions of Randolph (1935). The fixed root tips were dehydrated and mounted in paraffin by standard cytological procedures. A rotary microtome, set for a thickness of 11 mi-

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crons, was used for longitudinal sectioning of the root tips, and the resulting serial sections were stained with crystal violet-iodine stain and mounted on microscope slides. These slides were stored until measurements and counts could be made. The four groups of tips from each treatment were kept separate from each other throughout the procedure.

Measurements of cell size were made with the aid of an ocular micrometer mounted in a microscope. Magnifications of ocular and objective lenses were 10× and 43×, respectively. Under these conditions, one micrometer scale division was equivalent to 3.3 microns. Measurements were recorded to the nearest 0.1 scale division. Cells were measured in two regions of the root tip. For region I, measurements were confined to an area approximately 100 microns from the rather definite line separating the root cap from the remainder of the tip. Laterally, region I measurements were confined to the center portion of the section. There was little, if any, evidence of differentiation in this portion of the root tip. Lengths and widths (that is, the dimensions roughly parallel to the long axis of the root and at right angles to this axis, respectively) of five randomly-selected cells in one section from each tip were determined. Where possible, measurements were made on six tips from each of the four groups within each treatment. Thus, except in those instances where some tips were lost during the dehydrating, sectioning, mounting, and staining procedures, 30 cells per group, or 120 cells per treatment, were measured.

For region II, measurements of length and width were taken on cells lying approximately 650 to 850 microns from the line separating the root cap from the remainder of the tip. In this zone, considerable differentiation had occurred. Measurements were confined to the outer few layers of cells, where five randomly-selected pairs of cells were measured on a single section from each tip. Pairs of cells were used because, in this region, orientation of the cells made this procedure somewhat more convenient than measuring single cells. Each pair consisted of two cells adjacent to each other in the direction of the long axis of the root. Region II measurements were made on the same sections which were used for region I measurements.

An indication of the influence of the treatments upon mitotic activity was obtained by making counts of dividing cells in the root tip sections. As in the measurements of cell size, six tips per group (24 tips per treatment) were observed where possible. For each tip observed, counts were made on the terminal 330-micron portion of 10 individual sections. Thus, 240 sections per treatment were counted where possible. Cells which appeared to be undergoing any stage of mitosis were counted as dividing cells.

RESULTS AND DISCUSSION

Mean lengths of the primary roots from each treatment, and of the roots comprising the four groups within each treatment, are shown in table 1. At the particular seedling age which was used, distinct reduction of root length was observed only at the highest levels of X-rays or thermal neutrons. Ef-

TABLE 1

LENGTHS OF PRIMARY ROOTS USED IN STUDIES OF CELL SIZE AND MITOTIC ACTIVITY

Treatment	Number of useable seedlings	Length of primary root (mm.)				
		Group means				Treatment means and standard errors
		1	2	3	4	
Control	29	47.4	44.1	40.3	26.9	39.9 ± 1.72
10,000 r X-ray	30	49.5	42.1	36.4	26.6	39.1 ± 1.68
20,000 r "	30	42.9	39.0	35.0	26.3	36.1 ± 1.33
40,000 r "	32	36.6	35.4	31.4	19.8	30.8 ± 1.31
0.94×10^{13} $N_{th}/cm.^2$	32	45.6	41.9	36.0	26.8	37.6 ± 1.44
1.84×10^{13} "	31	46.4	41.9	36.4	29.4	38.8 ± 1.23
3.60×10^{13} "	29	43.0	35.6	35.0	17.7	33.2 ± 1.95

fects upon root length would doubtless have been more pronounced if a considerably longer germination time had been employed.

Mean dimensions of cells in the two regions described in the preceding section are presented in table 2, and counts of dividing cells are shown in table 3. Consideration of the group means disclosed no association between cell size or mitotic activity and root length within treatments; consequently, only treatment means are shown in the tables. No relationship of cell width to treatment is apparent from the data. With respect to cell length in both region I and region II, however, small increases were observed with increasing dose of either X-rays or thermal neutrons. In contrast to the apparently minor effect upon cell size, a rather drastic depressive effect of the treatments upon mitotic activity is indicated by the data.

TABLE 2

DIMENSIONS OF CELLS IN TIPS OF PRIMARY ROOTS FROM CONTROL AND IRRADIATED SEEDS OF MAIZE. REGIONS I AND II ARE DESCRIBED IN TEXT

Treatment	No. of determinations	Cell dimensions (μ)			
		Region I		Region II	
		Width	Length	Width	Length
		mean ± S.E.	mean ± S.E.	mean ± S.E.	mean ± S.E.
Control	120	16.3 ± 0.44	10.5 ± 0.25	18.4 ± 0.39	10.2 ± 0.47
10,000 r X-ray	100	16.9 ± 0.39	11.1 ± 0.34	16.6 ± 0.36	9.3 ± 0.46
20,000 r "	120	17.6 ± 0.42	10.9 ± 0.27	18.6 ± 0.32	10.6 ± 0.50
40,000 r "	120	15.8 ± 0.46	13.2 ± 0.35	18.3 ± 0.26	12.0 ± 0.64
0.94×10^{13} $N_{th}/cm.^2$	115	16.2 ± 0.44	11.1 ± 0.27	18.1 ± 0.37	10.1 ± 0.49
1.84×10^{13} "	120	16.3 ± 0.46	12.3 ± 0.32	18.5 ± 0.30	10.4 ± 0.59
3.60×10^{13} "	95	15.5 ± 0.57	13.0 ± 0.38	18.1 ± 0.33	10.8 ± 0.62

TABLE 3

NUMBER OF DIVIDING CELLS IN ROOT TIPS FROM CONTROL AND IRRADIATED SEEDS OF MAIZE

Treatment	Number of determinations	Number of dividing cells per section
		mean ± S.E.
Control	240	14.9 ± 0.42
10,000 r X-ray	200	9.7 ± 0.30
20,000 r "	240	6.7 ± 0.22
40,000 r "	240	5.8 ± 0.29
0.94×10^{13} $N_{th}/cm.^2$	230	9.0 ± 0.35
1.84×10^{13} "	240	6.0 ± 0.24
3.60×10^{13} "	190	3.8 ± 0.17

It would be expected that any treatment influencing cell number or cell size in the root would have an effect upon root length. Thus, irradiation-induced decreases in mitotic activity, and hence in cell number, would tend to reduce root length while irradiation-induced increases in cell length would tend to increase root length. With respect to root length in the present study, the effects of irradiation upon cell number and cell length partially offset each other. Schwartz and Bay (1956) noted that in root tips growing from maize seeds which had been subjected to extremely high doses (up to 500,000 r) of gamma rays, mitotic activity was completely arrested and the cells were much elongated.

In other work on the same lots of irradiated and control seed as were used in the experiments on cell size and mitotic activity, assays were made of the desoxyribonucleic acid (DNA) and ribonucleic acid (RNA) in the terminal 3-mm. portion of the root tip. A modification of the procedure of Ogur and Rosen (1950) was used for these assays. A tendency was observed toward decreased amounts of RNA per root tip with increasing dose of X-rays or thermal neutrons, but no consistent relationship was found between DNA content and dose. In view of the definite irradiation-induced depression of mitotic activity, the failure to detect significant reductions in DNA content in the irradiated material was rather surprising. Cell dimensions indicated, however, that differences between treatments with respect to number of cells in the terminal 3-mm. portion of the root were probably not great; thus, large differences in DNA content probably should not have been expected. If differences did indeed exist, they were not detected by the analytical procedures which were followed.

SUMMARY

Cell size, mitotic activity, and nucleic acid content were determined using tips of roots produced by the germination of control, X-irradiated, and thermal neutron-irradiated maize seeds. The dosage levels used had no

appreciable effect upon cell width, but small increases in cell length were associated with increasing dose of irradiation. The treatments effected drastic reductions in mitotic activity. A tendency was observed toward decreased amounts of ribonucleic acid per root tip with increasing dose of irradiation, but no consistent relationship was found between desoxyribonucleic acid content and dose.

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THE EFFECT OF S, 2-AMINOETHYLISOTHIURONIUM BROMIDE HYDROBROMIDE (AET) ON THE INDUCTION OF DOMINANT AND SEX-LINKED RECESSIVE LETHALS IN *DROSOPHILA MELANOGASTER*

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In recent years increased attention has been focused on protection of organisms, especially mammals, against acute radiation lethality by the injection of chemical compounds prior to irradiation. Of these compounds β-mercaptoethylamine (MEA) (Bacq and Herve, 1952), S, 2-aminoethylisothiuronium · Br · HBr (AET) and S, 3-aminopropylisothiuronium · Br · HBr (APT) (Doherty and Burnett, 1955; Doherty et al., 1957; Shapira et al., 1957) have been shown to afford the greatest protection against radiation death. Little is known, however, about the effectiveness of these compounds in protecting against induced genetic damage in the higher organisms. After the discovery that MEA is an effective protective agent against radiation death in mammals, Kaplan and Lyon (1953 a, b) reported that this compound did not protect against the mutagenic effect of X rays, either in Drosophila or the mouse. It seemed desirable to determine whether AET, which is a better protective agent than MEA on an equimolar basis, provided protection against the induction of dominant and sex-linked recessive lethals in *Drosophila melanogaster.*

In the dominant lethal experiments, Oregon-R males were injected intraabdominally with either saline or known amounts (0.15 μg and 0.30 μg) of AET that had first been dissolved in saline. Immediately after, or just prior to, injection the males were exposed to 4000 r of X rays (250 kvp; 30 ma; 3 mm of Al; hvl, 0.55 mm of Cu). After treatment, the males were pair-mated to virgin Oregon-R females for 24 hours. At the end of this mating period, the males and females were separated and the females were allowed to deposit eggs for two 24-hour periods. The males were mated immediately after separation to a second set of virgin females for 24 hours. At the end of this second mating interval, the males were discarded and the second set of females were allowed to lay for two 24-hour periods. The proportion of eggs that had not hatched (dominant lethals) in each sperm sample was determined by a count of uncollapsed eggs. The results of the three dominant lethal experiments are tabulated in table 1. Because a high degree of variability is characteristic of dominant lethal tests in *Drosophila melanogas-*

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TABLE 1

PERCENTAGE OF DOMINANT LETHALS INDUCED IN SPERM OF *DROSOPHILA MELANOGASTER* BY 4000 r OF X RAYS AFTER AET OR SALINE INJECTIONS

Experiment	Sperm Sample 1			Sperm Sample 2		
	Eggs laid	Unhatched eggs	% D.L.	Eggs laid	Unhatched eggs	% D.L.
Series 1 Preirradiation injection						
Saline	129	104	80.6	205	152	74.1
AET · Br · HBr, 0.15 μg	180	158	87.8	270	219	81.1
AET · Br · HBr, 0.30 μg	114	97	85.1	119	102	85.7
Series 2 Preirradiation injection						
Saline	245	206	84.1	563	414	73.5
AET · Br · HBr, 0.15 μg	130	113	86.9	484	385	79.6
AET · Br · HBr, 0.30 μg	214	183	85.5	524	443	84.5
Series 3 Preirradiation injection						
Saline	370	307	83.0	242	161	66.5
AET · Br · HBr, 0.30 μg	72	62	86.1	215	162	75.4
AET · Cl · HCl, 0.204 μg	186	161	86.6	325	250	76.9
Postirradiation injection						
Saline	295	249	84.4	387	253	65.4
AET · Br · HBr, 0.30 μg	335	285	85.1	333	215	64.6

ter, the raw data were tested for heterogeneity before analysis, and the conclusions presented in this paper are based on the results from that test. It is apparent from an examination of these data that there is a consistent, although slight, increase in the percentage of induced dominant lethals in the sperm of AET-injected flies as compared to saline-injected flies in sperm sample 1 in each individual experiment. In sperm sample 2, there is a marked increase in the percentage of dominant lethals in the AET-treated series in each of the three experiments performed. To determine whether this increase in induced dominant lethality might be caused by the bromine present in the AET compound, the chloride salt of AET was used. In series 3 of table 1 it can be seen that there is no difference in effect when equimolar amounts of AET · Cl · HCl are used instead of AET · Br · HBr. Furthermore, postirradiation treatment with AET indicates that the enhancement of X-ray mutagenicity occurs only if AET is present at the time of irradiation.

In the recessive lethal experiments, Oregon-R males were injected with either AET or saline and irradiated with 4000 r of X rays as in the dominant lethal tests. They were mass-mated immediately after treatment to virgin Muller-5 females in a ratio of ten females to one male, to maximize the number of progeny per injected male. Six days after mating, the males were removed from the females and discarded and the females were allowed to lay for an additional six days. Detection of sex-linked lethals was carried out in the usual manner. The results of this experiment are given in table 2. They indicate that the frequency of sex-linked recessive lethals induced by 4000 r of X rays in the sperm of Drosophila is higher in the AET-treated series than in the saline-injected controls. This conclusion is open to

TABLE 2

THE PERCENTAGE OF SEX-LINKED RECESSIVE LETHALS INDUCED IN SPERM OF *DROSOPHILA MELANOGASTER* BY 4000 r OF X RAYS AFTER INJECTION WITH AET OR SALINE

Injection	Chromosomes tested	Number of lethals	Percentage lethals
Saline	5174	522	10.09
AET	3618	480	13.27

question for technical reasons (although a chi-square test shows that the increase is significant) and is presented here mainly as corroboration for the dominant lethal tests.

Finally, a sex-linked lethal experiment was run to test for a possible mutagenic effect of AET *per se*. The control set was injected with saline, and the experimental set with AET; neither set was exposed to radiation. Numbers of lethal tests were selected such that a fourfold increase in the AET set over the control set would be detected with a probability of 0.9, and a chance deviation would be mistaken for such an increase in only one trial in a hundred. In the control set, the frequency of lethals was 0.0007 (5/6976) and in the experimental set, the frequency was 0.0008 (4/5030). On the basis of these results, the upper 90 per cent confidence limit for the ratio of experimental to control frequencies is 3.2, and the significance level of the observed difference is greater than 50 per cent.

DISCUSSION

These results present the curious situation that AET appears to enhance the lethal effects of radiation in Drosophila, although its effectiveness in preventing physiological death in the mammal is beyond question. In addition to the obvious explanation that the difference may reside in the nature of the biological mechanism involved, or in the inherent differences in the organisms, there exists the possibility that the somewhat greater amounts of radiation used in the Drosophila experiments is in some way involved.

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LETTERS TO THE EDITORS

Correspondents alone are responsible for statements and opinions expressed. Letters are dated when received in the editorial office.

COMMENT ON PROFESSOR STERN'S LETTER

Dr. Stern has kindly allowed me to see his article (Amer. Nat. 92: 313–316) before publication, and I should like to make one or two comments on it.

By emphasising the phrase "in this case" in the quotation from my book he implies that I consider the selection of sub-threshold genes as an explanation only for a special instance of genetic assimilation. This is not so. I should agree with him that it can be applied rather generally; but, as I made clear when discussing it on p. 170 et seq., I regard it as a "told to the children" version of what I wished to say. In my opinion it involves using the word "sub-threshold"—conventionally acceptable as it is—as a cloak to cover up all the more interesting questions. I think so for these reasons:

(i) A minor point is that "sub-threshold" tends to imply an all-or-none type of reaction, whereas it is essential to consider stress-response curves of other shapes.

(ii) Stern writes of genes which produce a certain phenotype in both environments A and B, but which can only be selected in environment B. This will usually be the case only if the genes have a stronger tendency to produce the phenotype in B than in A. If that is so, selection for the regular production of the phenotype in B will not necessarily result in its regular production when the stock is transferred back to A. The problem of why selection seems to go much further in B than is necessary—which I dealt with in terms of canalising selection—is not in fact solved by the mere invocation of sub-threshold genes without any elaboration of what they are supposed to be doing when they are below the threshold, or how they may modify the shape of the threshold.

(iii) The "sub-threshold" formulation is a bare, abstract concept, which to me looks rather thin when confronted with such a typical example of a pseudo-exogenous adaptation as, for example, the forelimbs of a digging animal like the mole. The environmental factors here, which set the levels of the thresholds, are the highly complex stresses involved in this mode of existence; the selection must operate, not on one or two genes, but on complicated genotypes which control responses within an elaborate network of developmental interactions and correlations. There is no obvious reason why thresholds of an all-or-none kind should be invoked in such cases, and it seems to me closer to the actual phenomena to discuss the matter in terms of genes which control the reactivity of the developmental system to the various stresses impinging on it. Moreover one can then use the same terms

to consider the problem of how selection brings into being genotypes which direct the response towards the optimum end-result, which may very well involve something more elaborate than a mere lowering or raising of all thresholds.

The points I have made are differences in mode of expression, rather than of substance, between Stern and myself. But in his summary he suggests a distinction, which I think to be an unreal one, between characters acquired on the basis of the general genotype of the species and those based on specific genotypes. I cannot attach any meaning to this. If any character is developed, under any circumstances, there are genes which have interacted with the environment to condition its development. I am certainly not suggesting that the genes on which genetic assimilation depends are of some special category outside the "general genotype" of the species.

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A COMPARISON OF PRODUCTIVITY IN A MUTANT AND WILD STRAIN OF TRIBOLIUM CASTANEUM HERBST*

As part of a project involving a study of selection in *Tribolium castaneum* populations, a preliminary investigation was made of the reproductive capacity of a mutant and wild strain. The mutant paddle (*pd*), derived by Park (1951) from a wild type stock maintained under laboratory conditions for many years, is a sex-linked recessive which results in a variable degree of fusion of the segments of the antennal club. The wild type stock used in the present experiments originated from a single female captured in 1955 in a storage bin containing rabbit pellets.

In a typical experiment eight adults, four males and four females not more than five days old, are placed in a vial containing one gram of medium consisting of 95 per cent sifted whole wheat flour and five per cent brewer's yeast. Ten such vials are prepared of the wild strain and ten of the mutant strain. The vials are kept at 29°C. and 65 per cent relative humidity. The beetles are allowed to deposit eggs in the vials for 20 days, are then transferred to a second set of vials for another 20-day laying period, and finally are transferred again for a third 20-day laying period. Sixty days after introduction of the parents into a vial the adult offspring are sifted out and counted. Since the life cycle of this species from egg to adult requires from 30 to 34 days, this collection schedule assures that from each 20-day laying period virtually all the offspring which reach the adult stage are counted.

*This investigation was supported in part by research grant RG-5406 from the National Institutes of Health, Public Health Service, and by a grant from the Permanent Science Fund of the American Academy of Arts and Sciences.

TABLE 1

THE NUMBER OF ADULTS RECOVERED FROM EACH VIAL AT THREE SUCCESSIVE 20-DAY LAYING PERIODS

Laying period					
1		2		3	
Wild	Mutant	Wild	Mutant	Wild	Mutant
36*	46	36	63	9	15
41	64	43	64	10	32
44	65	46	72	10	32
47	70	48	77	11	37
48	71	52	79	11	44
52	74	53	84	12	44
53	75	54	84	15	54
57	77	55	94	17	56
57	81	56	103	20	67
65	83	66	103	20	77
		Mean number per vial			
50.0	70.6	50.9	82.3	13.5	45.8
$t = 7.08$		$t = 19.04$		$t = 5.45$	
$P < 0.001$		$P < 0.001$		$P < 0.001$	

*Since there seemed to be no correlation between the numbers produced by each set of parents over the three periods, the data in these columns have been arbitrarily arranged in ascending order.

Table 1 contains the data from a single experiment which was repeated three times with essentially similar results. It is clear from a comparison of the mean number of adults recovered per vial in each laying period that there is a difference in the productivity of the two strains. During the three

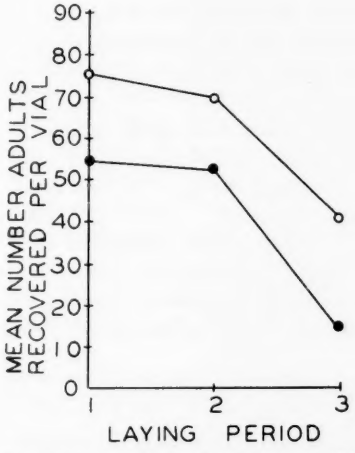

FIGURE 1. The decline in productivity of mutant and wild type beetles. o = mutant; • = wild type.

periods under consideration the wild type produced only 57.6 per cent as many offspring as the mutant. Figure 1 suggests that the only difference is in the numbers produced and not in the rate at which productivity declines.

The genetic basis for the difference in productivity has not yet been established. In this same species, Kollros (1944) found associated with the pearl mutation several effects which under certain conditions could influence productivity. It is conceivable, therefore, that the *pd* gene alone may be responsible. On the other hand, the difference may reside in the residual genotype of the two strains. In that case it is possible that the higher reproductive capacity of the paddle strain under the conditions of this experiment reflects its adaptation to a laboratory environment acquired over the many years it has been reared in captivity.

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LONG DURATION OF SPERM FUNCTION IN TWO EURYHALINE FISHES AND ITS LACK OF SIGNIFICANCE IN HYBRIDIZATION*

Many methods are used by animals to prevent or reduce the production of hybrids. In contrast with terrestrial animals, those breeding in water must be protected against chance meeting of gametes dispersed by the environment.

Clark Hubbs (1957) showed that sperm of one fish, *Percina caprodes* (Rafinesque), which has many known natural hybrids, retains its fertilizing capacity longer in heterospecific matings than does the sperm of another, *Etheostoma spectabile* (Agassiz), which has relatively few natural hybrids. As supplementary unpublished data supplement this information, the short temporal function of sperm of fresh-water fishes in the natural environment is thought to be an isolation mechanism. Carl L. Hubbs (1955) pointed out that hybrids among marine fishes are excessively rare when contrasted with

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those between north temperate fresh-water fishes. An isolation mechanism such as duration of sperm function could explain such a phenomenon by being much more effective in salt water than in fresh-water. Therefore, we have made some preliminary investigations to test this hypothesis. Our results with experiments strongly indicate that duration of sperm function does not act as effectively as an isolation mechanism in marine teleosts as it does in fresh-water teleosts. Although our work is with euryhaline rather than stenohaline marine teleosts we feel the results are applicable, especially since the known natural hybrids between euryhaline cyprinodonts occur in fresh-water (Hubbs, Walker, and Johnson, 1943). Moreover, generalizations are based on results from many experiments; therefore, additional tests must be made on a variety of fishes before these conclusions can be applied to fishes in general.

Other workers have demonstrated that sperm will retain their fertilization powers much longer in salt water than in fresh-water (Hoar, 1957; Rothschild, 1958); however, the work on teleosts concerns homospecific matings. As different results have been obtained between heterospecific and homospecific matings (Hoar, 1957, for non-teleosts, and our unpublished date on fresh-water teleosts) it was deemed necessary to test the hypothesis with heterospecific matings of salt water inhabiting teleosts.

The experimental fish were collected in the vicinity of Port Aransas, Texas. They were maintained under two environmental conditions, about 30°C. and 30 ppt salinity at Port Aransas and about 20°C. and 20 ppt salinity at Rockport. The results were comparable except that sperm appeared to function longer at Rockport, probably due to temperature effects (Lindroth, 1947). Sperm were stripped from the males following techniques described by Strawn and Hubbs (1956) into full 200 mm. preparation dishes (such dishes contain more than 1500 cc., which is assumed to be an adequate dilution for less than a drop of semen). Eggs were then stripped into the dish after an interval timed by a stop watch. Fertilization would occur no sooner than the timed interval and it might take longer for sperm to contact an egg in this dilution, thereby negative results might be due to chance.

Successful fertilization of *Fundulus grandis* Baird and Girard eggs with *F. similis* (Baird and Girard) sperm occurred after 40 seconds at 22°C. in Rockport and 37 seconds at 30°C. in Port Aransas as well as after shorter intervals. Successful fertilization of the reciprocal occurred after 31 seconds at 26°C. and 23 seconds at 28°C. both at Port Aransas. These times are much greater than those of 15 9 seconds at 15.5°C. and 21.3 at 21.3°C. for *E. spectabile* and *P. caprodes* reciprocals (Hubbs, 1957) especially when temperature effects on sperm activity (Lindroth, 1947) are considered. As all fish are intermediate between the parental types, parthenogenesis can be discounted.

Fertilization of *F. grandis* controls occurs after 58 seconds at 22°C. and 48 seconds at 27°C. indicating that homospecific matings can occur after the sperm have been exposed to the natural environment for longer intervals than occur with heterospecific matings.

Therefore, sperm of these euryhaline fishes retains its fertilizing powers for heterospecific matings much longer than that of tested fresh-water fishes. As the fresh-water fishes tested breed in rapids (Winn, 1958), it is possible that there is more need for them to prevent sperm dispersal; however, tidal currents in the Port Aransas region often reach 5 feet per second and we observed a current 0.5 feet per second at one of the stations where we collected our breeding stocks. These are only slightly less than those found in the rapids where the fresh-water species breed.

Some other isolation mechanism, therefore, may inhibit the production or development of natural hybrids in marine fishes. Hubbs (1955) suggested that the ephemeral and changing nature of the fresh-water environment contributed to the relatively high incidence of hybrids. This is clearly true when many marine habitats are compared with fresh-water environments; however, the sandy offshore islands near Port Aransas change greatly in configuration and environmental conditions change drastically with climatic conditions. Perhaps hybrid inviability is involved as certain cyprinodont hybrids including one of the reciprocal crosses here discussed, have a lower survival rate than their controls (Newman, 1914, and Hubbs and Drewry, in press) whereas hybrids among the fresh-water fishes tested seldom have lower survival rates than that of their controls (Hubbs and Strawn, 1957).

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ERRATA

p. 220	line	18	63	should read	65
	"	19	37	" "	35
236	"	26	*fertile*	" "	*sterile*
239	"	25	delete *autotrophic*		

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El-Ani, A. S., L. J. Klotz, and W. D. Wilson
should read
El-Ani, A. S., L. J. Klotz, and W. D. Wilbur

Hammons, L. M., G. Pontecorvo, and A. W. S. Bufton
should read
Hemmons, L. M., G. Pontecorvo, and A. W. S. Bufton

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